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CLASSIFICATION, RECONSTRUCTED PHYLOGENY, AND GEOGRAPHICAL HISTORY OF GENERA OF PILIPALPINAE (COLEOPTERA: TENEBRIONOIDEA: PYROCHROIDAE)

BY

DARREN A. POLLOCK

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

FALL, 1994

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ABSTRACT

The twelve genera of Pilipalpinae are classified based on characters of larvae and adults. Three new genera and six new species are here described: Malagaethes, gen. nov. (type species M. lawrencei, sp. nov.); Ranomafana, gen. nov. (type species R. steineri, sp. nov.); Binburrum, gen. nov. (type species Techmessa ruficollis Champion); Binburrum angusticollis, sp. nov.; Binburrum concavifrons, sp. nov.; Cycloderus immaculicollis, sp. nov.; Cycloderus hirsutus, sp. nov. The following new synonymies of specific names are proposed (with valid names given first): Paromarteon constans Lea 1917 = Eucistela cyanea Carter 1922; Paromarteon mutabile Blackburn 1897 = Paromarteon mutabile var. nigripenne Lea 1920; Temnopalpus bicolor Blackburn 1888 = Temnopalpus tricolor Lea 1920; Pilipalpus dasytoides Fairmaire 1876 = Copobaenus maculicollis Pic 1942 and Pilipalpus darwini Abdullah 1964. The following subspecies have been elevated to species rank: Paromarteon apicale Lea, Paromarteon fasciatum Lea, and Paromarteon parvum Lea.

Phylogenetic analysis of 30 structural characters of larvae and adults of Pilipalpinae (using Tydessinae, Pedilinae, and Pyrochroinae as outgroups) yielded the following set of incompletely resolved hypothetical relationships among genera of Pilipalpinae: (((Paromarteon + ((Temnopalpus + Malagaethes) + Pilipalpus + (Ranomafana + (Incollogenius + ((Exocalopus + (Binburrum + (Cycloderus + Morpholycus)) + Techmessodes) + Techmessa))))). The data set contained considerable homoplasy and several reversals.

The historical geographical relationships inferred from the reconstructed phylogeny were compared to geological evidence for the break-up of Pangaea and Gondwanaland. The ancestral stock of Pilipalpinae was widespread on Gondwanaland, and differentiated through its dissolution. Remnant relict genera persisted on Madagascar, New Zealand and Australia. Brooks Parsimony Analysis (BPA) was conducted on the data with the following area relationships: (Holarctic + (Madagascar + (New Zealand + (Australia + Chile)))). This agrees well with accepted geological evidence and is considered support for the hypothesized phylogeny. A single clade (Temnopalpus + Malagaethes) was in disagreement (homoplasous) with the area cladogram, indicating possible incongruence in the data. The area relationships of other southern hemisphere groups were compared with Pilipalpinae.

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A systematist benefits greatly from contacts, whether they contribute specimens, reprints, and / or advice. I have been very fortunate during my tenure at the University of Alberta, in that I have made contacts with many helpful persons. Foremost, I would like to thank my supervisor, George E. Ball, who made the project possible. Initially, he forced me to think carefully about both my project and future career plans before coming to Edmonton, but once I was accepted, both he and the entire department made me feel very welcome. Dr. Ball has been very generous with financial support and his enthusiasm; both are very much appreciated. I feel privileged to have been his student.

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Introduction

The classification of Tenebrionoidea is in a state of flux, and the relatively frequent changes in position of many taxa reflect their unstable classification. This situation is gradually improving, however, due in large part to greater enthusiasm for collection, description and analysis of immature stages of Coleoptera. The impressive chapter on Coleoptera larvae by Lawrence (1991) and the CD-ROM INTKEY system for beetle larvae identification (Lawrence et al. 1993) are indicative of the new, or at least heightened, interest in beetle larvae.

One group of families of Tenebrionoidea that has not had a very stable classification is, roughly, those of lineage (d) in Lawrence and Newton (1982: 282): Pythidae, Pyrochroidae, Pedilidae, Boridae, Mycteridae, Salpingidae, Inopeplidae, and Othniidae. Lawrence (1982) divided Pythidae into the subfamilies Pythinae and Pilipalpinae.

Watt (1987) used characters of both larvae and adults to reconstruct the phylogenetic relationships among Trictenotomidae, Salpingidae, Boridae, and Pythidae (sensu Lawrence 1982). Although self-admittedly preliminary, Watt's (1987) work is important in the systematics of a difficult section of Tenebrionoidea, because he used both larval and adult characters, and testable cladistic methods including explanation of rationale for character polarity assessment. Watt's study provided a useful basis for subsequent work on the group, including the present contribution.

Watt (1987) stated that because of certain similarities between Pythidae (especially Pilipalpinae) and Pyrochroidae, he had intended to combine these two groups as a single taxon of family rank. However, based on a re-evaluation of some characters, he considered similarities between Pythidae (Pilipalpinae) and Pyrochroidae to be convergent. Also, he hypothesized that the most pyrochroid-like Pilipalpinae (e.g. Exocalopus and Morpholycus) were the most derived in the subfamily. For the present study, I have adopted Watt's hypotheses of relationships of the salpingid group as a foundation, and therefore I have examined for comparative purposes, members of Pythinae, Boridae, Salpingidae (sens. Lawrence 1982) and Trictenotomidae, as well as Pyrochroidae.

It is unusual that another important paper was published regarding higher classification of the group of families around Pilipalpinae, since these taxa are rather obscure and generally have attracted little attention from systematists. Nikitsky (1986) published a paper dealing mainly with the genus Tydessa, but also with the elevation of Pilipalpinae to family status. It is obvious that Watt had not seen Nikitsky's paper, and Nikitsky had not seen Watt's. Both papers attempt to place the family Pythidae (or Pilipalpidae) among closely related families, using larval and adult characters. The major difference between the two papers is that Watt (1987) provided a phylogenetically-based rationale for his groupings, while Nikitsky (1986) did not. This is not to say that Nikitsky's paper is without value, but that his conclusions were not generally convincing.

I have attempted (Pollock 1994) to place Pilipalpinae in a phylogenetic framework, using as a starting point, the relationships hypothesized by Watt (1987). In my analysis, Pilipalpinae and Tydessinae are more closely related to Pyrochroidae (sensu stricto) than they are to Pythidae. Thus, my concept of Pyrochroidae is more inclusive than any published previously.

In summary, the various genera of Pilipalpinae were described in several families, and have only recently been assembled together in a single taxon (Crowson 1955; Lawrence 1982). This taxon has been named as a family (Nikitsky 1986), or placed in different families, most notably Pythidae (Lawrence 1982; Watt 1987) and Pyrochroidae (Crowson 1955), the latter of which, in my judgment, is preferable to the former.

This paper, an extension of Pollock (1994), treats the individual genera of Pilipalpinae. Although not the primary objective of this work, the species level taxonomy was studied, with new species described and synonymies proposed. Characters for

phylogenetic analysis and subsequent biogeographical analysis were selected from the adults, and, where available, from larvae, of genera of Pilipalpinae.

Material and Methods

Collections

This study is based on examination of 836 adults and approximately 780 larvae of Pilipalpinae, borrowed from the following collections, indicated by their respective codens alphabetically here, and in the text, as given in Arnett et al. (1993). Names of curators are in parentheses.

AAAC	Albert Allen Collection, 9235 Wenatchee Crescent, Boise, ID U.S.A83709
AMSA	Department of Entomology, The Australian Museum, 6-8 College Street, Sydney, N.S.W. 2000, Australia (M. Moulds).
ANIC	Division of Entomology, C.S.I.R.O., P.O. Box 1700, Canberra City, A.C.T. 2601, Australia; (J.F. Lawrence).
BPBM	Bishop Museum, 1525 Bernice Street, P.O. Box 19000-A, Honolulu, HI, U.S.A. 96817; (G.A. Samuelson).
CASC	Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, CA, U.S.A. 94118; (D. H. Kavanaugh & R. Brett).
CMNC	Entomology, Canadian Museum of Nature, P.O. Box 3443, Station D, Ottawa, ON Canada K1P 6P4; (R.S. Anderson).
CNCI	Canadian National Collection of Insects, Centre for Land and Biological Resources Research, Agriculture Canada, Ottawa, ON Canada K1A 0C6; (J. McNamara & L. LeSage).
DAPC	Darren A. Pollock, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada T6G 2E3.
DKYC	Daniel K. Young Collection, Department of Entomology, University of Wisconsin, Madison, WI, U.S.A. 53706.
FMNH	Division of Entomology, Field Museum of Natural History; Lake Shore Drive at Roosevelt Road, Chicago, IL, U.S.A. 60602 ; (A.F. Newton, Jr.).
MAIC	Michael A. Ivie Collection, Entomology Research Laboratory, Montana State University, Bozeman, MT, U.S.A. 59717
MCZC	Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A. 02138; (D.G. Furth).
MNHN	Entomologie, Muséum National d'Histoire Naturelle, 45 rue de Buffon, F-75005 Paris, France; (J.J. Menier).
MNNC	Museo Nacional de Historia Natural, Casilla 787, Santiago, Chile; (A. Camousseight M. & M. Elgueta D).
MVMA	Museum of Victoria, Natural History, 285-321 Russell Street, Melbourne, Vic. 3000, Australia; (A. Neboiss).
NDSU	Quaternary Insect Laboratory, Department of Geology, North Dakota State University, Fargo, North Dakota, U.S.A. 58105; (D. Schwert & A. Ashworth).
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. 20560; (T. J. Spilman & W.E. Steiner, Jr.).
NMNZ	National Museum of New Zealand, P.O. Box 467, Wellington, New Zealand; (R. L. Palma).
NZAC	New Zealand arthropod collection, Entomology Division, D.S.I.R., Private Bag, Auckland, New Zealand; (R.C. Craw).
QDPC	Entomology Branch, Department of Primary Industries, 80 Meiers Road, Indooroopilly, Qld. 4068, Australia; (K.J. Houston).

QMBA	Queensland Museum, P.O. Box 300, S. Brisbane, Qld. 4101, Australia; (G.B. Monteith).
QPIM	Department of Primary Industries, 28 Peters Street, Mareeba, Qld. 4880, Australia; (R.I. Storey).
RSMC	Richard S. Miller Collection, Entomology Research Laboratory, Montana
State	University, Bozeman, MT, U.S.A. 59717
SAMA	South Australian Museum, North Terrace, Adelaide, S.A. 5000, Australia; (E. Matthews).
UHGI	Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Bundesstrasse 55, 2000 Hamburg 13, Germany; (W.U. Weitschat).
UQIC	Department of Entomology, University of Queensland, St. Lucia, Qld. 4067, Australia; (M.A. Schneider).
WAMP	Department of Entomology, Western Australian Museum, Francis Street, Perth, W.A. 6000, Australia; (T.F. Houston).
ZMHB	Ausstellung Zoologie, Museum für Naturkunde der Humboldt-Universität, Invalidenstrasse 43, 1040 Berlin, Germany; (F. Hieke).

Taxa Examined for Comparison

In addition to specimens of Pilipalpinae, related taxa also were examined in this study. In the list of material examined that follows, an asterisk indicates examination of both adults and larvae for the given taxon. No asterisk indicates examination of the adult stage only. The classification used is that of Lawrence (1982), with composition of Pyrochroidae based on results of this study (see below).

TRICTENOTOMIDAE. Trictenotoma davidi Deyr. **SALPINGIDAE**. Rabocerus gabrieli Gerh., Sphaeriestes virescens (LeC.), Inopeplus dimidiatus Waterh., Elacatis Pasc. sp.* **PYTHIDAE**. Pythinae.—Pytho Latr. spp.*, Priognathus monilicornis (Rand.)*, Sphalma quadricollis Horn*, Anaplopus tuberculatus Blackb.* **BORIDAE**. Borinae.—Boros unicolor Say*, Lecontia discicollis (LeC.)*. Synercticinae.—Synercticus heteromerus Newman. **PYROCHROIDAE**. Tydessinae.—Tydessa Peacock spp. Pyrochroinae.—Dendroides Latr. spp.*, Neopyrochroa Blair spp.*, Schizotus Newm. spp.*, Pyrochroa Fabr. spp.*; Pedilinae.—Pedilus Fisch. spp.*

Measurements

Measurements, abbreviated as follows, and taken with a calibrated measuring ocular on a Wild M-5 stereomicroscope, are given in milimetres: **HL** - length of head from anterior margin of labrum to anterior margin of pronotum; **PL** - length of pronotum along midline, from anterior to posterior margin; **EL** - length of elytron from humerus to apex; **GHW** - width of head between outer margin of eyes; **GPW** - maximum width across pronotum; **GEW** - maximum width across both elytra. Where elytra are spread, or the specimen damaged, a single elytron was measured and this value doubled. As a general indication of size, the smallest and largest specimens available of each species were measured, and the values for **TL** (sum of HL, PL, and EL) and GEW are presented for the minimum and maximum.

To characterize the relative size of the larval urogomphi and urogomphal plate among genera, three ratios of measurements are given in the generic descriptions (see Fig. 233): **a/b** - ratio of urogomphal plate width to plate length, excluding urogomphi ; **a/c** - ratio of urogomphal plate width to plate length, including urogomphi; and **c/b** - ratio of urogomphal plate length, including urogomphi to plate length, excluding urogomphi.

Preparation of specimens

Dissections of male and female reproductive tracts follow the techniques of Pollock (1991). The entire abdomen was detached from specimens and macerated for several minutes in hot KOH solution. The internal female reproductive tract was dissected from the abdomen, and then stained in a saturated solution of chlorazol black (as suggested by Tschinkel and Doyen 1980), to improve the visibility of the bursa, glands, and spermathecae. Larvae were prepared for scanning electron microscopical examination as outlined in Pollock (1991).

Illustrations

Line drawings were executed in pencil using a WILD 1.25 x camera lucida fitted to a WILD M5 stereomicroscope, and later inked onto mylar film. Various dissected larval and adult structures were sputter-coated with gold to a depth of 15 nm; scanning electron micrographs were taken on a Cambridge Stereoscan at an accelerating voltage of 20 kV.

Localities

A list of localities is presented for each species examined, with the exception of several New Zealand species not examined in this study. In the list, the locality data are presented exactly as they appeared on the labels, with the exception that dates were converted to a standard format where unambiguous. Day of month is indicated by Arabic numerals, month by lower case Roman numerals, and the year fully written in Arabic numerals. Certain dates (e.g. 4-9-23) were left unconverted because they were ambiguous. Each symbol on the distribution maps represents a single collection, but for some species, a single symbol may represent several collections from localities too near one another to be indicated by separate symbols.

Rearing

Several taxa of Australian Pilipalpinae were reared successfully from larva to adult. The method used was essentially identical to that discussed by Pollock (1988). Clear plastic 35mm film canisters were used, into which was placed a quantity of the decaying inner bark material, and / or moistened paper towelling. Larvae constructed burrows in this material, and most eventually pupated and eclosed as adults. The best success was had with mature larvae of Morpholycus, of which more than 90 per cent survived to the adult stage. Larvae of Binburrum did not complete development in this system.

Descriptions

Generic descriptions for both adults and larvae were formatted and generated using DELTA (DEscription Language for TAxonomy) (Dallwitz et al. 1993; Askevold and O'Brien 1994). Characters are coded under each genus for individual states (ITEMS file), each of which is written out in a separate file (CHARS file). The program gathers the character states and arranges them for each taxon in language consistent with a taxonomic description. In this way, completely consistent descriptions were produced. The descriptions were edited subsequently to reduce the needless repetition of certain structures in the linkage series.

Terms and Abbreviations

Terms for adult and larval structures are the same as those in Lawrence and Britton (1991). Externally visible abdominal sternites in adults are referred to as ventrites. The first ventrite (V1) is actually the third abdominal sternite (S3). Several abbreviations are used in the text,

as follows: S9 — ninth abdominal sternum (adults and larvae); S8 — eighth abdominal sternum, etc. T9 — ninth abdominal tergum (adults and larvae), etc.

In most taxa of Pilipalpinae, elytral setae are of two distinct types. Setae arising from within, or slightly anterad, the large elytral punctures (termed the primary punctures) are termed primary elytral setae. Setae arising from between or amongst the primary punctures are called secondary elytral setae; these are inserted in smaller, secondary elytral punctures. In most taxa examined, the primary setae were decumbent, and the secondary setae erect.

Adults of certain genera have elytra that are relatively thin and lightly sclerotized (although they may be dark in colour). I have described these elytra as malacoderm-like, referring to the name Malacodermata, which is an old name for members of Cantharoidea and some Cleroidea. Adults of these groups generally have a relatively soft integument.

Males and females of all genera of Pilipalpinae have regular, stout antennal setae. Males of certain genera have the regular setae and also more slender, apically recurved setae. These latter setae are called male 2° setae in the text.

Nomenclature for wing veins and cells follows Kukalová-Peck and Lawrence (1993).

Type Specimens

Primary types were examined for all species except three species of Cycloderus, and all species of Techmessa, Techmessodes, and Exocalopus. Watt (1987) examined primary types for all New Zealand species, and I accepted his concepts for those species. Attempts to borrow the Fairmaire and Germain types of Cycloderus were unsuccessful.

Lectotypes were designated in circumstances where a holotype was not designated. Type specimens of taxa described by A.M. Lea are mounted on cardboard plates, many such plates with two or more specimens. For most species, Lea indicated the type with the letters 'TY', written on the cardboard plate. Any other specimens in the type series he referred to as co-types. In such situations, I have designated specimens indicated by 'TY' as lectotypes, and designated Lea's cotypes as paralectotypes.

For each primary type examined, label data are presented as they appear on the specimen. No differentiation between handwritten or typewritten labels was made. Type specimen label data are enclosed in quotations, and data from individual labels are separated by a slash (/). A space is left between the last character of one label and the first character of the next. Several labels actually have a slash, but in these situations, there are not spaces left between the characters separated by the slash. Where there is no information on a label, or if the information is illegible, descriptions of such labels appear in square brackets ([ ]). Therefore, any information presented in square brackets is not actually on the specimens, but has been added by me for descriptive purposes. I have not indicated the condition of the types, unless important for their identification as such.

Voucher specimens

During this study, several Australian pilipalpine taxa were reared from larva to adult. Voucher specimens of the various life stages of these species [Temnopalpus bicolor Blackburn, Morpholycus monilicornis Lea, M. costipennis Lea, and M. apicalis (Macleay)] are labelled as such, and are in the Australian National Insect Collection (ANIC), Canberra, Australia.

Criteria for ranking

I accept and follow the conventions used by various authors (e.g., Lawrence 1982; Watt 1987) for ranking family taxa in the salpingid group. The only major change adopted in this paper is the enlargement of Pyrochroidae to four subfamilies, each of which is

monophyletic and could be elevated to family rank. The relative ranks of all other taxa examined in this study are unchanged.

Genera were recognized on the bases of structural similarities (whether these be apomorphies or plesiomorphies), and inferred monophyly. Shape of antennomeres, and structure of male genitalia were useful in defining genera. All genera of Pilipalpinae are found on only one of the four southern hemisphere continental land masses. Therefore, a genus (for example, what was historically included in Techmessa) could not be present on both New Zealand and Australia. This geographic criterion was secondary and was not used to specifically delimit genera

For discrimination of species, I used not just one character system (e.g. male genitalia), but a suite of characters. Initially, I examined male genitalia to assess their relative merit as indicators of specific isolation. However, there were no obvious characters which would allow this, so I sought a more holomorphological species definition.

Within genera, important features (all of which were relatively constant among specimens examined) indicative of potential reproductive isolation were shape of antennomeres, shape and structure of pronotum, and shape of various structures on the male genitalia. For most genera, it was relatively easy to delimit species. For example, in Morpholycus, the combination of antennomere shape and shape of the male accessory lobes allows one to recognize six distinct species. Likewise in Cyclodenus, pronotal shape and elytral punctation was used to separate species. However, in genera such as Paromarteon and Temnopalpus, which are also known from relatively fewer specimens, such categorical decisions were more difficult to make. For these problematic genera, the criteria used are discussed individually, below. As well, my criteria for ranking at the suprageneric level are given below.

Methods for phylogenetic analysis

The methods employed here to infer phylogenetic relationships among genera of Pilipalpinae differ little from the modified Hennigian phylogenetic systematics espoused by Kavanaugh (1972), Wiley (1981), and many others. This method and the assumptions associated with it were critical to my analysis of the genus Pytho (Pollock 1991), and, despite criticisms, for example by Cronquist (1987) and Crowson (1991), cladistics has proven an effective method for hypothesizing genealogical relationship among taxa. I do not plan to defend the theoretical validity of cladistics; many authors have done so successfully. I discuss briefly, however, a common concern that I also share.

Several powerful computer programs (e.g. PAUP; HENNIG 86) generate cladograms once character state data are entered, based on various user-defined assumptions. Character polarities need not be determined before these data are entered (Swofford 1993), and hence, the computer acts as a 'black box', in which an algorithm(s) manipulates the data, and the tree(s) are produced. If the conclusions of one's entire phylogenetic analysis are based on a consensus tree derived from dozens or perhaps even hundreds of equally parsimonious trees, without explanation, or at least a vague understanding of how the program actually works, then these conclusions are suspect. Although the computer may seem to be totally objective, there is still the opportunity for the researcher to force personal biases on the analysis, through the use of relative character weighting and constraint trees. The computer analysis also may lead one to discover additional explanations of relationships which were obscured previously by less well-informed perceptions, or by rampant homoplasy in the data set.

The computer seemingly has become an indispensible tool in phylogenetic analysis, especially in the examination of many taxa of relatively higher rank, exhibiting homoplastic characters. Before I used the computer programs PAUP (Swofford 1993) and MacClade (Maddison and Maddison 1992), I had an idea of how the various taxa would group together. Once the computer analyses were run on PAUP, with generation of

numbers of equally parsimonious trees, these could be evaluated with MacClade. In this way, character state evolution could be evaluated graphically.

One of the problems associated with computer-derived phylogenies is the possibility of obtaining hundreds, or indeed thousands of equally parsimonious trees. For example, for 10 taxa, there are 2×10^6 possible unrooted, binary trees (Swofford 1993: 6). One can choose, and defend, one of the multiple trees, or choose to produce a consensus tree, which reflects information common to a group of similar trees, usually of equal length (Swofford 1993). Consensus trees have attracted attention from proponents (e.g. Bremer 1990; Anderberg and Tehler 1990) and detractors (e.g. Carpenter 1988; Miyamoto 1985). According to Anderberg and Tehler (1990), consensus trees should not be used as hypotheses of phylogeny, since they are based on tree topologies and not on actual characters. Wiley et al. (1991) suggest that strict consensus trees should be used with caution, but can be useful for determining which monophyletic groups are supported by all competing, equally parsimonious trees. I agree with that assessment.

Biogeographic methods

Several methods, outlined by Myers and Giller (1988), are available for elucidating the geographical history of a monophyletic taxon, and for comparing these histories. In recent literature, the exchanges between various proponents of these competing schools, notably cladistic biogeography versus panbiogeography (e.g. Heads 1985 versus Humphries 1985) resemble similar polemics between adherents of cladistics and phenetics. I have found that the tenets of cladistic biogeography follow most closely those of phylogenetic systematics. For analysis of Pilipalpinae, results of several recently developed analytical methods (e.g. Brooks Parsimony Analysis) were evaluated, in comparison to other taxa exhibiting distributions similar to that of Pilipalpinae. Details are presented below.

Systematic Position of Pilipalpinae and Composition of Pyrochroidae

The ten genera of Pilipalpinae (sensu Lawrence 1982) were placed originally in Oedemeridae, Melandryidae, Pyrochroidae, or Pedilidae. Several authors have commented on the placement of Pilipalpinae, and each offered different suites of characters to corroborate their differing views. The three competing hypotheses were: 1) that Pilipalpinae form a subfamily of Pythidae (Lawrence 1982; Watt 1987); 2) that Pilipalpinae should be allied with Pyrochroidae (sensu stricto) (Crowson 1955; pers. comm.); and, 3) that Pilipalpinae should be accorded family status (Nikitsky 1986).

In order to place Pilipalpinae in a phylogenetic framework and to determine the family placement of this taxon, Pollock (1994) examined the entire salpingid group of families, in both adult and larval stages, in order to determine the relationships of the constituent taxa. Five larval and 15 adult structural characters were analyzed. Features of the male and female genitalia, adult mouthparts, and larval urogomphal complex were especially useful.

Before using newly selected characters in a phylogenetic analysis, I re-analyzed the characters used by Watt (1987). His character states were coded as 0 (primitive) or 1 (derived), according to his own criteria (pp. 117-119), and entered into PAUP. To root the tree, a hypothetical ancestor with all states coded as 0 was included in the analysis (Table 1). In addition, Pyrochroidae (Pyrochroinae and Pedilinae) were added to the analysis, using Watt's characters. I included this taxon to see where Pyrochroidae would group with the families of Watt's salpingid group, according to his own criteria. An exhaustive PAUP search resulted in a single most parsimonious tree (Fig. 267). According to characters selected and used by Watt (1987), Pilipalpinae and Pyrochroidae are adelphotaxa, and both together are the adelphotaxon of Pythinae.

Next, I changed the polarities of the 18 characters used by Watt (1987) to reflect my own interpretations (Table 2). Another exhaustive search generated eight equally parsimonious trees. A strict consensus tree computed from these eight trees is given in Fig. 268. Information was insufficient to resolve the relationships among Boridae, Pythinae, Pilipalpinae, and Pyrochroidae. Because of this lack of resolution, I used different characters in the analysis of the relationships among Trictenotomidae, Salpingidae, Pythidae, Boridae, Pilipalpinae, and Pyrochroidae. For this analysis, the genus Tydessa (as Tydessinae) and the pyrochroid subfamilies Pyrochroinae and Pedilinae were coded separately. Twenty characters were selected from both larval and adult stages. PAUP was used to sort out the conflicting characters and to provide a starting point for subsequent more detailed mental analysis. The character matrix used for this analysis is given in Table 3. Discussion of the 20 characters is given by Pollock (1994).

The strict consensus cladogram in Fig. 269 differs in several very important aspects from the relationships postulated by Watt (1987) (Figs. 267-268). The genus Tydessa is separated from Pilipalpinae and placed as a taxon of subfamily rank. Based on shared possession of parameral struts, Trictenotomidae, Salpingidae, and Pythidae were supported as an unresolved monophyletic group. I found no character that would allow combination of the Trictenotomidae-Salpingidae-Pythidae complex to the rest of the salpingid group. Boridae and Pyrochroidae are adelphotaxa, and within Pyrochroidae, the subfamilies are arranged (Tydessinae + (Pilipalpinae + (Pyrochroinae + Pedilinae))).

The monophyly of (Pythidae + Boridae + Pyrochroidae) is not supported by the 20 characters examined in this study. Pythidae show closer relationship to Trictenotomidae and Salpingidae than they do to (Boridae + Pyrochroidae). In fact, Crowson (1981) combined Pythidae and Trictenotomidae, without explanation.

Although the family Pyrochroidae had remained fairly stable historically, there have been some significant changes to its composition and classification relatively recently. Young (1984) enlarged the family to include the Pedilinae: Pedilus, Anisotria, and Lithomacratria Wickh. (Florissant, late Eocene or early Oligocene). On the basis of similarities in structure of the urogomphal plate of Cononotus (Doyen 1979) and Agnathus Germ. (Mamaev 1976), Young and Pollock (1991) have suggested the inclusion of the genus Cononotus, and possibly Agnathus (as was done by Crowson 1981) in a taxon of subfamily rank within Pyrochroidae. Adults of both Cononotus and Agnathus are morphologically distinct from the remainder of the family but additional study of especially the adult stage is required before their inclusion in Pyrochroidae can be established. The family is further broadened in the present paper to include the subfamilies Tydessinae and Pilipalpinae, bringing the total of subfamily rank taxa to four.

One species of Pyrochroinae that is deserving of further study is Pogonocerus thoracicus Fisch., the sole member of this Palaearctic genus. Iablokoff-Khnzorian (1985) created the subfamily Pogonocerinae in Pythidae for this species, based on characters of the adult stage. From the figures provided in Iablokoff-Khnzorian (1985), this genus is clearly pyrochroine and does not belong in Pythidae. However, Mamaev (1976) and Kelejnikova and Mamaev (1981) illustrate the larva of Pogonocerus, showing some features unique among pyrochroines. The most obvious feature is the large, inner urogomphal tooth, which is found in all pythids and pedilines, most pilipalpines, but no other known Pyrochroinae. Also, the arrangement of the asperities along the anterior margin of sternite 9 is quite similar to that in Pilipalpinae or in Pedilus flabellatus Horn (Young and Pollock 1991). The separation of the ventral surface of the urogomphal plate into four distinct sections is very similar to the condition seen in larvae of Pilipalpinae. Pogonocerus is a distinct taxon and perhaps may be phylogenetically important in resolving generic relationships within Pyrochroinae.

Classification of Pilipalpinae

Pilipalpinae Abdullah

Type genus: Pilipalpus Fairmaire 1876

Pilipalpini Abdullah 1964b: 4
Pilipalpinae Lawrence 1982: 544
Pilipalpidae Nikitsky 1986: 1179
Pilipalpinae Watt 1987: 120
Techmessinae Paulus 1971: 84.

Type genus: Techmessa Bates 1874 (not stated by Paulus)

Adult stage

Diagnosis.—Penultimate and antepenultimate tarsomeres variously lobed and expanded laterally; tarsal claws with basal tooth; elytron in most taxa with conspicuous, mostly dimorphic, setae; median lobe without parameral struts, flat basally, with basal struts; apical maxillary palpomere variously cultriform; female bursa without accessory glands; spermathecal branches three in number, thin, threadlike.

Description.—Sexual dimorphism. Most genera exhibiting marked sexual dimorphism in one or more of: relative size of eyes, shape of antennomeres, relative lengths of antennomeres, and character of antennal vestiture. Of sexually dimorphic taxa, males with relatively larger eyes, relatively longer antennomeres, increased pectination of antennomeres [in Exocalopus (e.g. Figs. 10-11) and Morpholycus (Figs. 17-20)], and finer, denser, antennal setae ("male" antennal setae); no consistent sexual dichromatism noted within species.

Body form. TL approximately 3-15 mm; GEW approximately 1-5 mm; body elongate, subparallel-sided; elytra in most taxa widened slightly posterad midlength; body variously flattened dorsoventrally, with conspicuous dorsal vestiture in most genera and species.

Head. Head entirely visible dorsally, slightly to moderately narrowed behind eyes; GHW less than or subequal to GPW; frons flat, slightly convex, or concave; dorsum of head variously punctate, with setae of various lengths. Clypeus with anterior membranous area. Labrum transverse. Frontoclypeal suture variously developed, slightly depressed to distinctly carinate. Antennal insertions dorsolateral, entirely exposed, or partly concealed by supra-antennal crest in two genera. Eyes large, variously convex; in males of some taxa subhemispherical; convexity of eye symmetrical in most taxa; facets moderately fine to coarse, with short, inconspicuous intrafacetal setae; margin of eye entire or emarginate slightly, near antennal insertion (in Techmessodes only). Antennae (Figs. 1-20) elongate, sexually dimorphic in most taxa; scape robust, subcylindrical to subspherical; antennomere shape various, moniliform/subfiliform, elongate filiform, serrate, or pectinate. Mandibles (Figs. 38-67) asymmetrical, bidentate apically, with lateral margins variously arcuate from base to apex; terebral teeth absent; left mandible with premolar tooth, and with inner molar surface concave; right mandible without tooth, and with molar surface convex; mola of various sizes, well developed and subquadrate (Fig. 39), slightly developed and narrow (e.g. Fig. 42), or indistinct (Fig. 54) ; dorsal microtrichia present on mandibular base of some genera (e.g. Figs. 41, 56, 62); ventral surface of both mandibles with oblique, dense row of fine microtrichia in groove extended posteriorly to anterior extent of mola (Fig. 26, m); prostheca (Fig. 26, p) present, of various extent; mandibular scrobe with long setae. Maxilla. Galea broad, lacinia narrower, both fringed densely with very fine setae at their apices; palpus elongate, of 4 articles; palpomere 1 very small; palpomere 2 and 3 widened distally; palpomere 4 variously cultriform; palpomere 3 shorter than 2 or 4; palpomeres 2 and 3 with or without longer, finer setae on anterior margins; palpomere 4 with various number of digitiform organs dorsally.

Thorax. Prothorax subcircular to subquadrate, wider than long in most taxa; lateral margin smooth; pronotal disc evenly convex, flat, or with variously developed depressions on either side of midline; midline excavated, trough-like, in some taxa; lateral margins of disc entirely smooth, or with small marginal, setigerous tubercles; anterior margin of pronotum with or without distinct bead; posterior margin with bead in most taxa; margin trisinuate, laterally sinuate, or medially emarginate; in some taxa, basolateral margin of pronotum forming constricted collar with subparallel lateral margins; punctures of pronotum various, ranging from shallowly umbilicate (e.g. Fig. 92) to deeply faveolate (e.g. Figs. 100, 104). Prosternum transverse, wrinkled transversely and uniformly punctate in most taxa; prosternal process slender, knifelike, extended between but not posterad, procoxae. Elytra normally developed, in some taxa of flimsy malacoderm-like construction; epipleuron extended around elytral apex in some taxa (e.g. Fig. 136); traceable only to second or third ventrite in other taxa (e.g. Figs. 133-134); elytra flat to slightly convex dorsally, without longitudinal carinae or ridges in most taxa; punctation and vestiture various, in most genera uniform and dimorphic; large punctures with relatively shorter, adpressed setae (primary elytral setae) inserted just anterad punctures; smaller punctures with longer, erect setae (secondary elytral setae) (see Figs. 112, 114-115); posterior extent of sutural margin dentiform in one species, smooth in all others. Legs elongate, all pairs subequal in size and shape; tibiae slender, densely setose; tibial spurs short, 2-2-2; tarsi with penultimate and antepenultimate tarsomere emarginate to bilobed, with dense, fine setae ventrally; tarsal claw with basal tooth of various sizes; procoxae conical, variously projecting; protrochantins not visible; procoxal cavities open posteriorly and internally; mesocoxae narrowly separated by elongate mesosternal process, extended to metasternum; mesotrochantins exposed. Wings (Figs. 128-132) fully developed in all specimens examined; three or four anal veins in main group; second or third anal vein with wedge cell in most taxa; radial cell closed or open slightly; main crossvein (r4) entire or interrupted, indistinctly developed; medial fleck variously developed in most taxa; M + Cu extended to posterior wing margin. Metendosternite with distinct laminae and anterior tendons.

Abdomen. All ventrites non-connate; ventrites uniformly punctate / setose except for muscle attachment areas in some taxa; posterior margin of S7 entire in females, variously emarginate in males. Male genitalia. S8 emarginate along posterior margin; T8 with posterior margin entire; S9 with paired, lateral sclerites plus elongate spiculum; in all genera except one (Pilipalpus), branches of spiculum separate; aedeagus with bipartite tegmen of distal apicale and proximal basale (Figs. 137-148); in repose, medial lobe laterad, dorsad or ventrad tegmen; apicale and basale subequal in length, or with one distinctly longer than the other; apicale cleft in some taxa (e.g. Figs. 137, 143; accessory lobes inserted at various positions along apicale; some taxa with accessory lobes inserted at apex of apicale (e.g. Figs. 139, 141, 144); others with accessory lobes inserted more proximally (e.g. Figs. 137, 143); accessory lobes various in shape - from subquadrate (Figs. 162-165) to elongate and slender; setation of accessory lobes various. Female genitalia. Ovipositor elongate, only slightly sclerotized, flexible; styli subcylindrical, inserted subapically; setae on styli apical only; coxites uniformly pubescent, divided transversely into several sections; ventral valviferal and coxital baculi, and dorsal proctigeral baculi distinct, slender; valviferal baculi in several taxa with lateral, accessory sclerotization near midlength; spiculum gastrale slender, not forked; bursa copulatrix simple, sac-like, without accessory glands or ducts (Figs. 177-184); spermathecae elongate, threadlike, three in number, attached distad median oviduct; exterior of bursa with denticles in three genera (Figs. 177, 183).

Larval stage

Diagnosis.—Head with two stemmata per side (except for Techmessa); urogomphal plate with two urogomphal pits (Figs. 225-226, 232-233); urogomphi with 3 or fewer tubercles per side, without transverse series of tubercles; single inner urogomphal

tooth, or tooth absent (in Exocalopus, Fig. 233); urogomphal plate and abdominal tergites with punctulae.

Description.—Body shape orthosomatic, elongate, parallel-sided; body lightly sclerotized except for head, tarsunguli, and abdominal segments 8 and / or 9; generally sparsely and simply setose, with recognizable serial pattern; body variously flattened dorsoventrally.

Head prognathous, lateral margins rounded to subangulate (Figs. 202-208), moderately well sclerotized. Epicranial suture distinct, frontal arms lyriform, extended to near antennal insertions; epicranial stem absent, or very short; endocarinae absent. Frontoclypeal suture present, or at least suggested; labrum separate from clypeus; antennal fossa narrowly separated from dorsal mandibular articulation; ventral epicranial ridges present. Two stemmata (none in Techmessa), arranged horizontally near antennal fossa; anterior stemma slightly more ventrad; stemmata with pigment spots and slightly convex lenses; pigment spots appearing almost confluent, lenses separated by diameter of single lens. Labrum transverse, with various number of medial and marginal setae. Epipharynx with fine microtrichia medially; tormae elongate, longitudinal, and symmetrical, hooked distally. Hypostomal rods absent, or short and posteriorly divergent. Antennae elongate, 3-segmented; scape widest, antennomeres progressively narrowing to flagellum; antennomeres cylindrical, distinctly longer than wide; sensorium of various shape, flattened elliptical, dome-like, or conical; setae generally distributed or present only at apices of antennomeres; flagellum with long apical seta at least half length of flagellum. Mandibles (Figs. 209-214) distinctly sclerotized, moderately stout, slightly asymmetrical; dorsal carina with various number of smaller, blunt teeth; molae well developed, consisting of transverse ridges, present on both mandibles though distinctly asymmetrical; left mola straighter and more vertical, with large premolar tooth at its distal extent (Fig. 209); right molar surface convex; mandible surface smooth, except for mola, and two conspicuous setae along lateral margins of mandible; dorsal surface of mandible with rows of microtrichia of various lengths (Fig. 213). Ventral mouthparts retracted, cardines far posterad ventral mandibular articulations. Maxillae well developed; stipes elongate, longer than wide, at least three times length of cardo; maxillary articulating area well developed, larger than cardo; maxillary palpi three-segmented, with few fine, scattered setae; distal area of stipes forming mala; mala with long, stout setae apically and along internal (ventral) margin; mala with shallow, apical cleft; mala bearing distinct uncus, with three teeth, the innermost of which is larger than other two, in some taxa. Ligula paraboloid, anterad very short prementum; labial palpi of two palpomeres, subequal in length to ligula; prementum with or without single, short seta posterad each palpus; mentum only slightly sclerotized in anterior half; posterior half of mentum with pair of setae; submentum with pair of setae near midlength. Hypopharynx distinct; hypopharyngeal sclerome large, distinctly sclerotized.

Thorax with pro-, meso- and metathorax subquadrate, subequal in length. Prothorax relatively narrower, meso- and metathorax subequal in width; cervicosternum divided longitudinally in three sections, with incomplete division of outer two; cervicosternum (presternum?) extended posteriorly to level of procoxae; lateral margins of prothoracic tergite straight or subangular; lateral margins of meso- and metathoracic tergites rounded; mesothoracic spiracle conspicuous, annular; spiracular laterotergite variously produced outward from body wall; long setae present at anterolateral corners and at hind angles of prothoracic tergite; meso- and metathoracic tergites with long setae along lateral margins; meso- and metathoracic tergites with or without distinctly sclerotized parabasal ridges. Legs relatively long and slender, subequal in size and shape; coxae widely separated; front legs oriented anterolaterally, middle and hind legs oriented laterally; setae fine, sparsest on trochanter and femur, more dense on tibia; tarsungulus single, well developed, about half length of tibia; femur with single, long seta on distoventral margin.

Abdomen of ten segments; segments 1-7 subequal in size and shape, similar to meso- and metathorax; parabasal ridges present or absent on T1-T8; parabasal ridges sinuous or relatively straight, joined mesally or not; spiracles small, annular, with crenulate peritremes; T1-T7 with smooth surface, with evidence of small punctulae along lateral margins of T7 in some taxa; long setae along lateral margins posterad spiracle, and along posterior margin; shorter setae along posterior margin of abdominal sterna; abdominal segment 8 subequal in length to 7, or distinctly longer; T8 with punctulae and/or areas of more distinct sclerotization toward lateral margins; posteroventral margin of T8 rounded evenly, or developed into dentiform process; S8 with series of 3 short setae on each side, along posterior margin. Urogomphal plate (Figs. 215-226) distinctly sclerotized, with distinct dorsal macrosculpturing of punctulae and/or wrinkling; T9 bearing pair of posteriorly directed, immoveable urogomphi of various shape; inner urogomphal teeth present or absent, if present, then single tooth on each urogomphus; urogomphal teeth of various lengths and positions of attachment on urogomphi; dorsal surface of T9 with 2 setigerous tubercles on or near base of each urogomphus; lateral and ventral margins of urogomphi with various number of long setae, borne on small tubercles; intra-urogomphal process various, entirely absent or conspicuously produced posteriorly; urogomphal pits present in most taxa, if so, then paired; pits with or without accessory processes; basolateral margins of T9 wider than, or subequal in width to, lateral margins of urogomphi; T9 extended ventrally, forming four distinct plates; inner margins of plates variously thickened or lobate; S9 rectangular, wider than long, and less distinctly sclerotized than T9; S9 with variously developed, transverse arch of minute to small, distinctly sclerotized asperities; outer pair of asperities distinctly larger than others; arch without gap medially, but variously emarginate or not; S9 with setae along lateral margin; anus transverse, situated between S9 and plates of T9.

Key to Genera of Pilipalpinae Based on Adults

1(0). Elytral epipleuron short, not traceable to near apex of elytron (e.g. Figs. 133-134 2

Elytral epipleuron distinct, traceable to at least near apex of elytron (e.g. Figs. 135-136).....5

2(1). Elytra with both scattered suberect to erect secondary, and dense subrect to decumbent primary setae (e.g. Figs. 109, 115); primary elytral punctures conspicuous; antennae filiform to submoniliform (Figs. 2-3, 6) 3

Elytra with conspicuous long erect secondary setae, and inconspicuous decumbent primary setae (Fig. 112); primary elytral punctures small, indistinct; antennae moniliform to subserrate (Fig. 1); distribution —Australia .....Paromarteon Blackburn

3(2). Antennomeres distinctly filiform (Fig. 6); pronotal disc with 2 rows of large, umbilicate punctures laterad midline with extensive glabrous areas; distribution —Chile.....Pilipalpus Fairmaire

Antennomeres approaching submoniliform (Figs. 2-3); pronotal punctures comparatively finer, not arranged in 2 rows laterad midline; pronotal disc without large glabrous areas; distribution —Australia or Madagascar.....
.....4

4(3). Lateral margins of pronotal disc with three setigerous tubercles per side, basally; pronotal disc evenly convex dorsally; distribution —Madagascar .....
.....Malagaethes, gen. nov.

Lateral margins of pronotal disc without tubercles basally; pronotal disc flattened or only slightly convex dorsally; distribution —Australia .....
.....Temnopalpus Blackburn

5(1). Head and pronotum with deep, faveolate punctures, areas between punctures carinate (e.g. Figs. 98, 100, 104); body generally of larger size.....11

Head and pronotum with coarse, umbilicate punctures, areas between punctures flat to rounded (e.g. Figs. 88, 90, 92); body generally of smaller size.....6

6(5). Antennae pectinate in males, serrate in females (Figs. 10-11); head with distinct arcuate carina between clypeus and frons; head and pronotum (Fig. 89) with variously sized glabrous areas medially; distribution —New Zealand.....Exocalopus Broun

Antennae filiform in both sexes; head without frontoclypeal carina; head and pronotum uniformly punctate.....7

7(6). Eyes emarginate anteriorly around antennal insertions; distribution —New Zealand.....Techmessodes Broun

Eyes not emarginate anteriorly; distribution —New Zealand, Madagascar, and Australia.....8

8(7). Distribution—Australia or New Zealand.....9

Distribution—Madagascar.....10

9(8). Pronotum rounded to angulate at widest point, near midlength (e.g. Fig. 85); pronotal depressions distinct (in most species), oblique; antennomere III subequal in length to IV (Fig. 7); distribution —Australia.....Binburrum Pollock, gen. nov.

Pronotum (Fig. 87) widest anterad middle with smoothly arcuate lateral margins; pronotal depressions indistinct; length of antennomere III less than length of IV (Fig. 8); distribution —New Zealand.....Techmessa Bates

10(8). Pronotal margin with several setigerous tubercles, mostly in posterior half.....Ranomafana Pollock, gen. nov.

Pronotal margin smooth, without setigerous tubercles.....Incollogenius Pic

11(5). Antennomeres elongate, filiform (Fig. 12); elytra black, contrasting lighter coloured pronotum; pronotal disc with rounded lateral margins (Figs. 95, 97, 99); distribution —Chile and adjacent Argentina.....Cycloderus Solier

Antennomeres shorter, moniliform, serrate or pectinate (Figs. 13-20); lycid-like in colouration, elytra with contrasting pattern of black and orange (in most specimens); pronotal disc with subparallel to slightly rounded lateral margins (Figs. 101, 103, 105); distribution —Australia .....Morpholycus Lea

Key to Genera of Pilipalpinae Based on Larvae

1(0). Inner urogomphal tooth absent (Fig. 233) .....Exocalopus Broun

Inner urogomphal tooth present (e.g. Figs. 218-220), various in size and shape 2

2(1). Inner urogomphal teeth relatively short, triangular (Figs. 215; 234), positioned near base, or about midlength of urogomphi; distribution—Australia.....3

Inner urogomphal teeth relatively long, curved anteromesally (e.g. Figs. 216-220), positioned in most specimens at, or posterad, half length of urogomphi; distribution—various 4

3(2). Intra-urogomphal process produced posteriorly (Figs. 227-231); inner urogomphal teeth positioned near base of urogomphi.....Temnopalpus Blackburn

Intra-urogomphal process not produced posteriorly (Figs. 234-235); inner urogomphal teeth positioned near midlength of urogomphi.....Paromarteon Blackburn

4(2). Distribution—Australia 5
Distribution—Chile and New Zealand 6

5(4). Anterolateral angle of urogomphal plate produced as dentiform process (Fig. 216); thoracic spiracular laterotergite distinctly produced in most specimens (Fig. 204); urogomphi each with three long setae ..... Binburrum Pollock, gen. nov.

Anterolateral angle of urogomphal plate not so produced (Figs. 218-220); thoracic spiracular laterotergite not distinctly produced (Fig. 208); urogomphi each with greater than three long setae ..... Morpholycus Lea

6(4). Stemmata absent; urogomphal pits large, narrowly separated by intra-urogomphal process; urogomphi relatively short, outer margins distinctly convergent posteriorly; asperities along anterior margin of S9 absent; distribution—New Zealand ..... Techmessa Bates

Stemmata present; urogomphal pits small, separated by relatively wide urogomphal lip; urogomphi longer, outer margins subparallel or only slightly convergent posteriorly; asperities along anterior margin of S9 present; distribution—Chile or New Zealand 7

7(6). Urogomphal pits separated by greater than length of single urogomphus (Fig. 232); dorsal margin of urogomphal pits without triangular process; distribution—New Zealand ..... Techmessodes Broun

Urogomphal pits separated by less than length of single urogomphus (Fig. 216); dorsal margin of urogomphal pit with triangular process (Fig. 225); distribution: Chile ..... Cycloderus Solier

Genus Paromarteon Blackburn

Figs. 1, 38-40, 112, 128, 133, 137, 149, 177, 190, 202, 234-235, 238, 270

Paromarteon Blackburn 1897: 94.—Lea 1917: 167.—1921: 216.—Csiki 1924: 55.
Type species: Paromarteon mutabile Blackburn 1897: 95 (by monotypy)

Eucistela Carter 1922: 79.—Carter 1930: 270, 272.—Doyen et al. 1989: 238, 252
Type species: Eucistela cyanea Carter 1922: 80 (by monotypy) (= Paromarteon constans Lea 1917). **NEW SYNONYMY.**

Notes on synonymy.—Doyen et al. (1989) stated that Eucistela is probably congeneric with Paromarteon, which was corroborated by this study; hence, these names are synonyms of one another.

Adult

Diagnosis.—Antennomeres (Fig. 1) submoniliform in both sexes; head and pronotum with few scattered, shallow punctures (Figs. 83-84); pronotal disc convex, without depressions; lateral margins rounded; elytra sparsely and shallowly punctate, primary setae indistinct, secondary setae erect (Fig. 112); epipleuron indistinct (Fig. 133); distribution: Australia.

Description.--Body small, moderately convex; TL 3.4-6.0 mm; GEW 0.9- 2.3 mm; vestiture conspicuous, sparse.

HEAD. Punctation inconspicuous, largely absent. Antennae (Fig. 1), not sexually dimorphic, antennomeres of equal shape and length in males and females; antennomeres 4-10 submoniliform; antennomere 3 and 4 subequal in length; male 2° setae absent; antennomere 2 moniliform. Mandibles (Figs. 38-40). Mandibular mola large, subquadrate (Fig. 39); lateral margin of mandible evenly arcuate to apex (Figs. 38, 40); ventral microtrichial row relatively long, microtrichia long; dorsal mandibular ornamentation absent; apex moderately produced; eye slightly to moderately convex in both sexes, ocular margin

entire; frontoclypeal suture arcuate, distinctly impressed line. Maxilla with palpomere 4 slightly cultriform, almost subsecuriform.

PRONOTUM (Figs. 83-84), transverse (GPW/PL 1.40-1.55), lateral margins widest near midlength; disc with lateral margin evenly arcuate, evenly convex dorsally; posterior margin slightly emarginate medially; depressions absent; punctation of disc very sparse, (punctures separated by many times their own diameters); anterior and posterior beads carinate.

ELYTRA (Fig. 112) thin, malacoderm-like, without longitudinal ridges or carinae; epipleuron (Fig. 133) traceable to abdominal sternite 3 or anterad, narrow; primary setae very short, at most 1/10 length of secondary setae, inserted within primary punctures; secondary setae uniformly distributed among primary setae; primary punctures very small, longitudinally elliptical; microsculpture absent.

MALE GENITALIA (Figs. 137, 149). Aedeagus in repose with tegmen oriented ventrad median lobe; apicale longer than basale or subequal in length to basale, deeply cleft distally; accessory lobes slender, sub-parallel sided, greater than half length of apicale, inserted toward base of apicale; median lobe relatively slender, subacutely pointed, lateral margins subparallel-sided, tapered gradually distally, smooth throughout entire length.

FEMALE GENITALIA (Fig. 177). Spermathecae elongate, extended outside of ovipositor; bursa copulatrix with external denticulae basally.

Taxonomic notes.—Lea (1917) examined the type specimens of P. mutabile and identified a distinct resemblance between that species and Temnopalpus bicolor Blackburn, both genera of which were included originally among the Australian Melandryidae. Lea (1917) mentioned several colour forms of P. mutabile, and described P. constans from northern Queensland. Four years later, Lea (1921) described formally these and other colour forms as varieties of P. mutabile, three of which (P. apicale, P. parvum and P. fasciatum) were collected in Brisbane and / or on Bribie Island, and the other (P. nigripenne) being more widespread through Victoria, N.S.W., and southern Queensland.

It was very difficult determining the taxonomic status of each of Lea's (1921) varieties of P. mutabile. I evaluated several character systems. The male genitalia was of some use in recognizing putative species of Paromarteon. For example, P. constans has a comparatively small and stout aedeagus, with the accessory lobes extended distally past the apicale. This is unique for the genus. Also, the genitalia of P. parvum are distinct enough to warrant species status. Differences among the genitalia of the remaining four species are more difficult to discern and evaluate. Among these forms, P. apicale and P. fasciatum are probably distinct species. Their genitalia are similar to each other but different from those of P. mutabile and P. nigripenne. The genitalia of P. mutabile and P. nigripenne are indistinguishable.

The second criterion used was colour, although this character is quite variable in many of the genera and species of Pilipalpinae examined. It was combined with the third criterion, geographical distribution. Four of the species are very constant in body colour, and also have restricted ranges, based on the relatively few specimens examined (see diagnoses for P. constans, P. parvum, P. fasciatum, and P. apicale). Typical P. mutabile has been collected only in Victoria, while P. nigripenne is comparatively widespread; these two forms differ from each other only by colour of the elytra, the former of which is testaceous, and the latter piceous. Numerous specimens exhibit a colour intermediate between these two extremes. Based on these criteria, the name P. nigripenne Lea is synonymized with P. mutabile Blackburn, and the remainder of Lea's (1921) varieties are treated as distinct species. I feel that species status for P. constans, P. parvum, P. apicale, and P. fasciatum is justified. However, the status of P. mutabile and P. nigripenne and the specimens exhibiting a colour between these two forms are tentative. Possibly P. nigripenne is a valid species, or P. apicale may be a colour variety of P. mutabile. Additional

specimens, especially from southern Queensland, and rearing and associating of larvae, may help solve this minor taxonomic problem.

Larva

Methods of association.—The presumed larvae of Paromarteon were neither reared to adult, nor collected in association with adults. Based on the combination of character states exhibited by the specimens, these larvae cannot be placed in any of the other three Australian genera of Pilipalpinae. Therefore, the specimens are presumed to represent a species of Paromarteon, pending successful rearing and association of larvae and adults of this genus.

Diagnosis.—Distribution: Australia; outer margins of urogomphi smooth, without conspicuous tubercles; urogomphi each with three long setae; intra-urogomphal process absent; urogomphal pits very small.

Description.—HEAD (Fig. 202) with lateral margins evenly, slightly arcuate, subparallel basally; stemmata two per side; hypostomal rods absent; ratio of antennomere lengths (1:2:3): 0.6:0.9:0.8; antennal sensorium moderately raised, subconical; setae on antennomere 2 sparse, apical only; setae on antennomere 3 relatively sparse, in apical third of antennomere; apical antennal seta greater than or equal to 1/2 length of antennomere 3.

THORAX (Fig. 202). Thoracic parabasal ridges present; spiracular laterotergite not distinctly produced laterally; lateral margins of prothorax subparallel basally, then divergent anteriorly in anterior 1/3; margins of prothorax with one long and one short seta at anterolateral corner, 1 seta at posterolateral corner; lateral margins of meso- and metathoracic terga with one elongate seta.

ABDOMEN. Abdominal parabasal ridges slightly arcuate; basolateral areas of T8 and entirety of urogomphal plate darkly pigmented; punctulae distinct, uniform on T9, on posterolateral corners of T8; terga with no setae adjacent to spiracle; three lateral marginal setae; segment 8 from 1.0-1.2 x length of segment 7; posterolateral angle on T8 smooth, without dentiform process.

UROGOMPHAL PLATE (Fig. 234-235). Anterior corner of T9 smooth, not produced into blunt dentiform process; a/b = 2.18; a/c =1.28; c/b =1.71; urogomphi with three elongate and one shorter setae, lateral margins subparallel, without tubercles; apices distinctly upturned subapically only; basolateral urogomphal flange slightly produced laterally, with two elongate setae per side; dorsum of urogomphal plate with 3 small tubercles arranged in triangle on base of urogomphi; anterior tubercle only, setigerous; inner urogomphal teeth present, medium size, curved outwardly or straight; inserted slightly anterad midlength of urogomphi; intra-urogomphal projection broadly rounded, slightly arcuate posteriorly; urogomphal pits extremely small, distinctly circular, separated by 8-10 x width of single pit, with evenly sclerotized dorsal and ventral margins; asperities on S9 distinctly tooth like, not coalesced.

Unassociated larval material examined.—**New South Wales**. Wollomombi Falls, 40 km E. Armidale, 1978-1979, R. Noske, (ANIC, 2). **Victoria**. 34.41S 142.18E, 9 km NNE Hattah 25.x-3.xi.1988, T. Weir, J. Lawrence & M. Hansen, from mallee bark, (ANIC, 3).

Natural history

Compared to other Australian genera of Pilipalpinae, almost nothing is known of the natural history of members of Paromarteon. Label data on examined specimens do not support their being collected using the usual methods (flight intercept traps, malaise traps, blacklight, etc.), indicating that they may behave somewhat differently compared with the other three genera. Two presumed larvae of Paromarteon were collected from under Eucalyptus (Myrtaceae) bark in the mallee region (Victoria), indicating that species of the genus may be found also in the drier regions of eastern Australia, and are not restricted to the moister rainforest.

Two specimens of P. apicale were mounted on the same cardboard plate with two specimens of an unidentified alleculine tenebrionid, were mounted together on the same cardboard plate. The alleculines are coloured exactly the same as the Paromarteon, except that the alleculine has an entirely testaceous head. This may suggest a mimicry complex involving P. apicale.

Geographical distribution (Figs. 238-239)

The genus is restricted to Australia; specimens have been collected in Victoria, New South Wales, and Queensland. It is apparently absent from Tasmania.

Relationships (Fig. 270)

Paromarteon is the most basal genus of Pilipalpinae in the reconstructed phylogeny, constituting the adelphotaxon of the remainder of Pilipalpinae. Primitive adult features include moniliform antennae (character 22) (Fig. 1), pronotal disc without depressions (character 25) (Fig. 83), abbreviated elytral epipleuron (character 6) (Fig. 133), and elongate accessory lobes inserted basally on the apicale (character 12) (Fig. 137).

Key to species of Paromarteon Based on Adults

1(0). Dorsal surface dark, with bluish metallic lustre; known only from north Queensland.....P. constans Lea
Dorsal surface with at least pronotum lighter in colour, without metallic lustre; known from southern Queensland, New South Wales, and Victoria.....2

2(1). Elytra testaceous basally with variously developed apical infuscation, extended 1/2 to 2/3 length of elytron.....3
Elytra entirely testaceous, entirely piceous, or testaceous with transverse black fasciae.....4

3(2). Head testaceous; size smaller, TL 3.4 - 3.5 mm; known only from Bribie Island, SE Queensland.....P. parvum Lea, stat. nov.
Head dark basally; size larger, TL 4.1 - 6.0 mm; more widely distributed in SE Queensland.....P. apicale Lea, stat. nov.

4(2). Elytra testaceous with two transverse fasciae in apical half; size smaller, TL 3.5 mm; known only from Bribie Island, SE Queensland.....P. fasciatum, stat. nov.
Elytra entirely testaceous or piceous; size larger, TL 3.9 - 5.1 mm; known from Victoria, New South Wales, and S. Queensland.....P. mutabile Blackburn

Paromarteon apicale Lea, stat. nov.
Figs. 38-40, 83-84, 112, 128, 137, 149, 177, 190, 238

Paromarteon mutabile, var. apicale Lea 1921: 217. TYPE MATERIAL: LECTOTYPE (SAMA), male; labelled: "Bribie I. Moreton Bay Lea & Hacker / Type of var apicale / mutabile var. apicale Queensland [this label with 'TYPE' in red ink along right margin] / S.A. Museum Specimen / LECTOTYPE (left specimen) & PARALECTOTYPES Paromarteon mutabile var. apicale Lea design. D.A. Pollock 1991". PARALECTOTYPES (SAMA): 3 specimens, one male mounted upside down, 2 females (one mounted upside down) on same cardboard plate as lectotype. 4 specimens, 2 males, 2 females (1 mounted upside down); labelled: "Bribie I. Moreton Bay Lea & Hacker / Bribie I. Moreton Bay Lea & Hacker / Co-type / mutabile var. apicale Queensland [this label with 'Cotype' in red ink along right margin] / S.A. Museum Specimen / PARALECTOTYPES Paromarteon mutabile var. apicale Lea design. D.A. Pollock 1991". TYPE LOCALITY: Australia, Queensland, Bribie Island.

Specific epithet.—A Latin adjective derived from the noun apex, pertaining presumably to the apical dark markings on the elytra.

Diagnosis.—Dorsum of head black posteriorly, testaceous anteriorly; elytron with apical piceous area, occupying less than half length of elytron; pronotum distinctly transverse, GPW:PL > 1.5, GPW:GHW > 1.25; known only from the Brisbane area, S. Queensland.

Description.—TL 4.1-6.0 mm; GEW 1.4-2.3 mm. Head. Dorsum of head piceous to black posteriorly, anterior extent of dark colour between midlength of eye and antennal fossae; antennomeres 1-3 or 4 pale, antennomeres 4 or 5 - 11 infuscated; antennomeres 4-5 only slightly darkened; venter of head pale except for genae infuscated in some specimens. Prothorax. Ratio of GPW:PL (n=20) 1.55; ratio of GPW: GHW (n=20) 1.26; pronotum uniformly testaceous; prosternum testaceous. Elytra. Elytra testaceous with apical half (at most) infuscated; anterior margins of dark apical markings slightly arcuate to truncate across elytra; dark colour not extended anteriorly along suture. Male genitalia. Aedeagus relatively large; apicale distinctly longer than basale; accessory lobes extended to near distal end of apicale; accessory lobes slender, parallel-sided, with all distal setae of approximately equal length.

Geographical distribution (Fig. 238).—Paromarteon apicale is apparently restricted to southern Queensland, most specimens having been taken in the Brisbane area.

Material examined.—In addition to the types, I examined 82 specimens from the following localities: **Queensland**. Brisbane, H. Hacker, 4.9.1911, (QMBA, 4); 9.ix.1912, (MVMA, 4; QMBA, 1); 11.9.1912, (QMBA, 1); 10.8.1913, (QMBA, 5); 3.9.1915, (QDPC, 3); 5.9.1916, (QMBA, 4); 26.ix.1916, (QMBA, 3); 7.9.1926, (QMBA, 6); Brisbane, Ix.1933, J.G. Brooks Collection, (DAPC, 1; ANIC, 1); Brisbane, McGregor, (SAMA, 2); Brisbane, Acacia Ridge, 17.ix.1964, A.N., (MVMA, 1); Brisbane, Illidge, (UQIC, 2); Brisbane, Sunnybank, xi.1926, W.A. Summerville, (QDPC, 2); Brisbane, no other data, (UQIC, 2; BMNH, 3); Sunnybank, 16.ix.1929, (QDPC, 1); 25.09S 151.11E 24 km NbyE Eidsvold, 11.x.1984, I. Naumann & J. Cardale, (ANIC, 1); Camira, near Ipswich, 27°38'S 152°55'E, 13.ix.1985, G. Daniels, (UQIC, 28); Stradbroke I., collector's initials illegible, (MVMA, 4); Bribie Island, Moreton Bay, Lea and Hacker, (MVMA, 3); Beerburrum, S.E. Qld, 9.ix.1971, E.C. Dahms, (QMBA, 1).

Paromarteon constans Lea

Figs. 1, 238

Paromarteon constans Lea 1917: 168. TYPE MATERIAL: LECTOTYPE (SAMA), sex unknown; labelled: "constans Lea, Type Cairns / I 6117 Paromarteon constans Lea Queensland [this label with 'TYPE' in red ink along right margin] / S.A. Museum Specimen / LECTOTYPE (left. spec.) & PARALECTOTYPES Paromarteon constans Lea design. D.A. Pollock 1991". PARALECTOTYPES (SAMA): 2 males, 1 sex unknown mounted on same card as lectotype. 3 specimens on one cardboard plate, 2 females (?), 1 male; labelled: "Cairns dist. F.P. Dodd / Co-type / 18850 Paromarteon constans Lea Queensland [this label with 'Cotype' in red ink along right margin] / right specimen (male) dissected / S.A. Museum Specimen / PARALECTOTYPES Paromarteon constans Lea Design. D.A. Pollock 1991". TYPE LOCALITY: Australia, Queensland, Cairns District.—Csiki 1924: 55.

Eucistela cyanea Carter 1922: 80. TYPE MATERIAL: LECTOTYPE (MVMA), female; labelled: "Cairns dist. F.P. Dodd / TYPES / Type ♂♀ / Eucistela cyanea Id. by H.J. Carter / H.J. Carter Coll. P. 20.4.22 / LECTOTYPE (left spec.) ♀ Eucistela cyanea Carter design. D.A. Pollock 1991". PARALECTOTYPES: 2 females (?) (MVMA) on same plate as lectotype. 1 specimen (ANIC), sex unknown; labelled: "Cairns dist. F.P. Dodd / Co.TYPES H.J.C. [this label written in black ink, except 'Co' and the capital

'S' at the end of 'TYPES', in red ink] / Eucistela cyanea Carter ld. by H.J. Carter / PARATYPE / PARALECTOTYPE Eucistela cyanea Carter design. D.A. Pollock 1991". TYPE LOCALITY: Australia, Queensland, Cairns District.—Carter 1930: 272.—Doyen et al. 1989: 252. **NEW SYNONYMY**

Specific epithet.—From the Latin adjective constans, meaning uniform or invariable, probably because of the uniform dark metallic colouration of all specimens examined by Lea.

Diagnosis.—Dorsal surface uniformly piceous with blue or violaceous metallic lustre; accessory lobes of male genitalia short, each with three very long, distal setae; known only from the Cairns district, N. Queensland.

Description.—TL 3.5-4.3 mm; GEW 0.9-1.5 mm; body uniformly piceous with distinct bluish or violaceous metallic lustre; antennomeres 1 and 2, mouthparts, and tarsi somewhat lighter in colour. Pronotum. Ratio of GPW:PL (n=7) 1.40; ratio of GPW:GHW (n=7) 1.13. Male genitalia. Aedeagus relatively small; apicale slightly longer than basale; accessory lobes extended beyond distal end of apicale; accessory lobes short, widened slightly at about their midlength; lobes each with three very long distal setae, in addition to other shorter setae.

Geographical distribution (Fig. 238).—Paromarteon constans is apparently restricted to northern Queensland; only the type specimens (of both Paromarteon constans and Eucistela cyanea) from the Cairns District are known.

Material examined.—Type material, only. See above, for details.

Paromarteon fasciatum Lea, stat. nov.
Fig. 238

Paromarteon mutabile, var. fasciatum Lea 1921: 217. TYPE MATERIAL: HOLOTYPE (SAMA), male; labelled: "Bribie I. Moreton Bay Lea & Hacker / Type of var fasciatum / mutabile var fasciatum Queensland [this label with 'TYPE' in red ink along right margin] / S.A. Museum Specimen / HOLOTYPE Paromarteon mutabile var. fasciatum Lea". PARATYPE (SAMA), male; labelled: "Bribie I. Moreton Bay Lea & Hacker / Co-type / mutabile var fasciatum Queensland [this label with 'Cotype' in red ink along right margin] / S.A. Museum Specimen / PARATYPE Paromarteon mutabile var. fasciatum Lea". TYPE LOCALITY: Australia, Queensland, Bribie Island.

Specific epithet.—From the Latin noun fascia, meaning a band or a stripe, indicative of the transverse elytral band on specimens of this species.

Diagnosis.—Size smaller (TL 3.5 mm); head rufopiceous; elytron testaceous with apical, paired, transverse fasciae; accessory lobes of male genitalia slender, extended to near distal end of apicale; known only from Bribie Island, S. Queensland.

Description.—TL 3.5 mm; GEW 1.2 mm (only one specimen in adequate condition for measurement). Head. Dorsum of head entirely rufopiceous; clypeus and labrum lighter, rufotestaceous; antennae testaceous to antennomere 5, then gradually and progressively infuscated; venter of head rufous, lighter than dorsal; ventral mouthparts testaceous. Pronotum. Ratio of GPW:PL 1.48; ratio of GPW:GHW 1.07. Elytra. Elytra testaceous with two transverse fasciae in apical half; anterior fascia extended to lateral margins, posterior fascia not extended to lateral margins; both fasciae slightly less darkly pigmented across elytral suture. Male genitalia. Aedeagus relatively large; apicale distinctly longer than basale; accessory lobes extended slightly beyond distal end of apicale; accessory lobes elongate, slender, with all distal setae of approximately equal lengths.

Geographical distribution (Fig. 238).—All examined specimens of Paromarteon fasciatum were collected on Bribie Island, in Moreton Bay, southern Queensland.

Material examined.—Type material, only. See above, for details.

Paromarteon mutabile Blackburn

Figs. 133, 239

Paromarteon mutabile Blackburn 1897: 95. TYPE MATERIAL: HOLOTYPE (BMNH), sex unknown, prob. female; labelled: "[round 'Type' label with red/orange border] / Paromarteon mutabile, Blackb". PARATYPE (SAMA), male; labelled: "Paromarteon mutabile Blackb. co-type / I. 6092 Paromarteon mutabile Blkb Victoria. [this label with 'Cotype' written in red ink along right margin] / S.A. Museum Specimen / PARATYPE Paromarteon mutabile Blackburn". TYPE LOCALITY: Australia, Victoria, Alpine region [?].—Lea 1917: 167.—1921: 216.—Csiki 1924: 55.

Paromarteon mutabile, var. nigripenne Lea 1921: 217. TYPE MATERIAL: LECTOTYPE (SAMA), female; labelled: "Brisbane: H. Hacker 11/9/12 \ Ty of Var nigripenne / mutabile var. nigripenne Lea Q: N.S.W: [this label with 'TYPE' in red ink along right margin] / S.A. Museum Specimen / LECTOTYPE (left spec.) & PARALECTOTYPE Paromarteon mutabile var. nigripenne Lea Design. D.A. Pollock 1991". PARALECTOTYPES (SAMA): 1 male mounted on same plate as lectotype; 3 specimens on same pin: 2 specimens, left one male, right one female, mounted on same plate; 1 male mounted on other plate beneath; labelled: "Tamworth / Co-type / mutabile var. nigripenne Q: N.S.W: V: [this label with 'Cotype' written in red ink along right margin] / S.A. Museum Specimen / PARALECTOTYPES Paromarteon mutabile var. nigripenne Lea design. D.A. Pollock 1991". TYPE LOCALITY: Australia, Queensland, Brisbane. **NEW SYNONYMY**

Specific epithet.—From the Latin adjective mutabilis, meaning changeable, in reference to the variation of colour exhibited by the type series.

Diagnosis.—Elytron entirely pale, entirely piceous, or variously bicoloured.

Description.—TL 3.9-5.1 mm; GEW 1.1-1.7 mm. Head. Dorsal head colour various, from entirely testaceous to entirely piceous; some specimens with only posterior half piceous; antennae pale to antennomere 3-5, distal antennomeres variously infuscated; ventral head colour various, with at least gula testaceous. Pronotum. Ratio of GPW:PL 1.49 (n=20); ratio of GPW:GHW 1.17 (n=20); entire prosternum testaceous. Elytra. Elytra entirely pale, entirely piceous, or variously bicoloured. Male genitalia. Aedeagus relatively large; apicale distinctly longer than basale; accessory lobes extended to near distal end of apicale; accessory lobes elongate, widened slightly toward apex; all distal setae of approximately equal length.

Taxonomic notes.—As P. mutabile is recognized here, it includes at least two more or less distinct colour forms, one being typical P. mutabile, and the other corresponding to variety nigripenne of Lea (1921). The typical form is restricted to Victoria, while the darker form is more widespread, and is found in Victoria, New South Wales, and in southern Queensland.

Geographical distribution (Fig. 239).—The geographical range of Paromarteon mutabile is extensive, from Victoria to Queensland.

Material examined.—In addition to the types, I examined 72 specimens, from the following localities: **Victoria**. Cockatoo, 12.31, Goudie, (ANIC, 1); Gippsland, no other data, (MVMA, 8 T); Gippsland, Drouin [prob. collector], (MVMA, 2); Killara, 21.xi.20, C. Oke, (MVMA, 2); Warburton District, no other data, (MVMA, 4); Healsville district, no other data, (ANIC, 1), (MVMA, 1); Bayswater, xi.1928, (ANIC, 2); Bayswater, 26.xi.1928, J.E. Dixon, (MVMA, 2); Moorooduc, 13.xi.1920, (MVMA, 3; ANIC, 3); Narbethong, 22.i.1949, F.E. Wilson, F.E. Wilson Collection, (MVMA, 1); Pakenham, C. Oke, (MVMA, 2); Beaconsfield, 2.12.1917, F.E.W. [F.E. Wilson?], F.E. Wilson Collection, (MVMA, 1); Dividing Range, no other data, Blackb's Coll., (SAMA, 6); Emerald, 28.x.1907, Jarvis, (SAMA, 1); Rowville, 10.28, J.C. Goudie, (MVMA, 1); Frankston, 10.33, J.C. Goudie, (MVMA, 2), (ANIC, 1); Croydon, no other data, (MVMA, 1); Benalla, Helms, (SAMA, 1); Buff. [may be Buffalo], no

other data, (SAMA, 1); state record only, no other data, (MVMA, 1). **New South Wales**. Dorrigo, W. Heron, (SAMA, 1); Upper Williams River, x.1926, Lea & Wilson, (MVMA, 1); Tamworth, 9.10:92, Lea, (SAMA, 2); Nambucca River, H.J. Carter Coll., P. 20.4.22, (ANIC, 1); 19 km W. Dubbo (32.15S 148.37E), 29.ix.1971, on fls., S. Misko, (ANIC, 3); 9 km N. Sutton, 12.ii.1971, S. Misko, (ANIC, 1); Blackheath, Blue Mts. 3000 ft., i.1932, Darlington, Harvard Australia Expedition, (MCZC, 1); Sydney, no other data, (AMSA, 1). **Queensland**. Blackall Rgs., x.1920, F.E. Wilson, (MVMA, 1); Toowoomba, 26.xi.1974, J. Macqueen, (ANIC, 1); ditto, 30.xi.1974, J. Macqueen, (ANIC, 1); Brisbane, 11.9.1912, H. Hacker, (SAMA, 2); ditto, 5.9.1916, H. Hacker, (QMBA, 3); Bunya Mts., 2000', 14.xii.1937, N. Geary, (AMSA, 1); Brisbane, Illidge, (UQIC, 2): Sunnybank, 16.ix.1929, (QPIM, 2).

Paromarteon parvum Lea, stat. nov.

Fig. 238

Paromarteon mutabile, var. parvum Lea 1921: 217. TYPE MATERIAL: HOLOTYPE (SAMA), male; labelled: "Bribie I. Moreton Bay Lea & Hacker / Type of var parvum / mutabile var. parvum Lea Queensland [this label with 'TYPE' in red ink along right margin] / S.A. Museum Specimen / HOLOTYPE Paromarteon mutabile var. parvum Lea". PARATYPES (SAMA), 2 females, mounted on same plate, right specimen upside down and badly damaged; labelled: "Bribie I. Moreton Bay Lea & Hacker / Co-type / mutabile var parvum Queensland [this label with 'Cotype' in red ink along right margin / S.A. Museum specimen / PARATYPES Paromarteon mutabile var. parvum Lea". TYPE LOCALITY: Australia, Queensland, Bribie Island.

Specific epithet.—From the Latin adjective parvum, meaning small or short, indicative of the relatively small size of this species compared to most other species of Paromarteon.

Diagnosis.—Size small, TL 3.4-3.5 mm; head, pronotum and elytra testaceous except for apical half of elytron piceous; accessory lobes extended well beyond distal end of apicale; known only from Bribie Island, S. Queensland.

Description.—TL 3.4-3.5 mm; GEW 1.2-1.3 mm. Head. Dorsum of head testaceous; antennae infuscate from antennomere 5. Pronotum. Ratio of GPW:PL 1.47 (n=2); ratio of GPW:GHW 1.08 (n=2). Elytra. Elytra testaceous with apical piceous area occupying approximately apical half of elytra; dark area not extended anteriorly along suture. Male genitalia. Aedeagus relatively small; apicale slightly longer than basale; accessory lobes extended well beyond distal ends of apicale; accessory lobes relatively short and stout, widened distally; all distal setae of approximately equal lengths.

Geographical distribution (Fig. 238).—Paromarteon parvum is known only from Bribie Island, in Moreton Bay, southern Queensland.

Material examined.—Type material, only. See above, for details.

Genus **Temnopalpus** Blackburn

Figs. 2, 41-43, 113-114, 129, 134, 138, 150, 178, 191, 203, 215, 221, 227-231, 240-242, 270

Temnopalpus Blackburn 1888: 285. TYPE SPECIES: Temnopalpus bicolor Blackburn 1888 (by monotypy)—Lea 1917: 162.—Csiki 1924: 55.

Adult

Diagnosis.—Antennomeres short filiform - submoniliform in both sexes (Fig. 2); lateral margins of pronotal disc rounded, widest near midlength; head and pronotum with widely spaced, small, shallowly umbilicate punctures; elytra with indistinct epipleura (Fig. 134); distribution: Australia.

Description.— Body small, distinctly depressed; TL 3.5-5.6 mm; GEW 1.1-2.0 mm; vestiture conspicuous.

HEAD. Punctation umbilicate, sparse. Eye slightly to moderately convex in both sexes, ocular margin entire; frontoclypeal suture arcuate, distinctly impressed line. Antennae (Fig. 2) not sexually dimorphic, antennomeres of equal shape and length in males and females; antennomere 2 moniliform; antennomeres 4-10 submoniliform; antennomere 3 and 4 subequal in length; male 2° setae absent. Mandibles (Figs. 41-43). Mandibular mola narrow, widest anteriorly, narrowed posteriorly; lateral margin angulate subapically; ventral microtrichial row relatively short, microtrichia long; dorsal surfaces with microtrichia near base; apex moderately produced. Maxilla with palpomere 4 moderately cultriform.

PRONOTUM (Fig. 191) circular, lateral margins widest near midlength; disc with lateral margin evenly arcuate, flat dorsally; posterior pronotal margin truncate; pronotal depressions absent from most specimens, others with indistinct small depressions; punctation of pronotal disc uniform, shallowly umbilicate (punctures separated by 1-2 x their diameters); anterior and posterior pronotal beads marked by small punctures.

ELYTRA (Fig. 113-114) thin, malacoderm-like, without longitudinal ridges or carinae; epipleuron traceable to V3 or anterad, narrow; primary setae elongate, greater than half length of secondary setae, inserted anterad primary punctures; secondary setae uniformly distributed among primary setae; primary punctures very small, longitudinally elliptical; microsculpture absent.

MALE GENITALIA (Fig. 138, 150). Aedeagus in repose with tegmen oriented ventrad median lobe; apicale subequal in length to basale, or shorter than basale, entire distally; accessory lobes slender, sub-parallel sided, less than half length of apicale, inserted toward apex of apicale; median lobe relatively slender, blunt, rounded, lateral margins subparallel-sided, tapered gradually distally, smooth throughout entire length.

FEMALE GENITALIA (Fig. 178). Spermathecae elongate, extended outside of ovipositor; bursa copulatrix without external ornamentation.

Taxonomic notes.—Recognition of species of Temnopalpus was rendered difficult by several factors, including distinction of T. niger and T. tricolor primarily on colour. If colour is not used as a taxonomic character, there is little separating the three described species. The holotype of T. bicolor exhibits relatively short, and distinctly moniliform antennomeres, while those of all other specimens exhibiting a similar colour pattern are only slightly moniliform, and are relatively longer. Therefore, is the holotype of T. bicolor a different species from all other bicoloured specimens? In all other genera of Pilipalpinae, antennomere shape is constant within species, but the type of T. bicolor may be aberrant.

Some differences in male genitalia were noted among bicoloured specimens, and Tasmanian and Victorian specimens of T. niger. It was difficult to decide whether or not these differences are indicative of species status. There seemed to be as much difference between the genitalia of T. bicolor and Tasmanian T. niger as there was between Tasmanian and Victorian T. niger. Also, specimens of T. niger from Victoria and T. niger from Tasmania differed distinctly in size, with those of the former considerably smaller.

Examination of the larvae (see "taxonomic notes, below) provided evidence that there are at least two species of Temnopalpus. Additional rearing is needed to determine if these other larval types (especially types 2, 4, and 5; see below) do in fact yield adults distinct from T. bicolor. Also, adults from Western Australia are needed in order to obtain an adult associate for larval type 5.

Given the evidence and specimens at hand, I have synonymized T. tricolor and T. bicolor. Lea (1920) described this species based only on colour, and I have been unable to find consistent structural difference between the holotype of T. tricolor and other bicoloured specimens. Temnopalpus niger was described on the basis of structural as well as colour characters, although the former are very slight.

Larva

Method of association.—Larvae have been collected in association with adults (ANIC), but rearing from larva to adult had not been done previously to confirm this association. I reared larvae collected under bark of Nothofagus cunninghamii (Hook. fil.) Oerst., to the adult stage, for confirmation of the generic larval-adult association.

Diagnosis.—Distribution: Australia; thoracic and abdominal tergites without parabasal ridges; lateral areas of T8 more heavily sclerotized than remainder of tergite; inner urogomphal teeth very short (Figs. 215, 227-231); inner urogomphal teeth positioned basally or medially on urogomphi; intra-urogomphal process variously produced, angulate at lateral corners (Figs. 227-231); urogomphal pits indistinct, only slight concavities.

Description.—HEAD (Fig. 203). Lateral margins evenly arcuate, subparallel-sided medially; stemmata two per side; hypostomal rods absent; ratio of antennomere lengths (1:2:3): 0.6:0.8:0.6; antennal sensorium slightly raised, dome-like, subelliptical; setae on antennomere 2 generally distributed, of uniform lengths; setae on antennomere 3 relatively sparse, in apical third of antennomere; apical antennal seta greater than or equal to 1/2 length of antennomere 3.

THORAX (Fig. 203). Parabasal ridges absent; spiracular laterotergite not distinctly produced laterally; lateral margins of prothorax evenly, slightly divergent anteriorly, slightly emarginate near midlength; margins of prothorax with two setae at anterolateral corner, 1 seta at posterolateral corner; lateral margins of meso- and metathoracic terga with two elongate setae.

ABDOMEN. Parabasal ridges absent; posterolateral margins of T8 and urogomphal plate concolorous, darkly pigmented; punctulae distinct, uniform on T8, marginal on T7; terga with no setae adjacent to spiracle; three lateral marginal setae; segment 8 from 1.0-1.3 x length of segment 7; posterolateral angle on T8 smooth, without dentiform process.

UROGOMPHAL PLATE (Figs. 215, 221, 227-231). Anterior corner of T9 smooth, not produced into blunt dentiform process; a/b = 1.87; a/c = 1.22; c/b = 1.53; urogomphi with four elongate and one shorter, setae, lateral margins slightly convergent posteriorly, with single tubercle near base; apices distinctly upturned subapically only; basolateral urogomphal flange distinctly produced laterally, with two elongate setae per side; dorsum of urogomphal plate with 1 small tubercle on urogomphi, near inner tooth, and 1 seta slightly anterad base of urogomphi; inner urogomphal teeth present, very small, triangular, inserted near base of urogomphi; intra-urogomphal projection broad, with angulate lateral angles and variously arcuate posteriorly; urogomphal pits relatively small, subelliptical, outer margin indistinct, separated by less than, or width of single pit; urogomphal pits with more heavily sclerotized dorsal margin; asperities on S9 distinctly tooth like, not coalesced.

VARIATION. There are five larval types among material examined: **LARVAL TYPE 1** (Fig. 227).—Intra-urogomphal process wide, not produced greatly; inner urogomphal teeth very small, blunt; this type was reared from material collected at Cambarville, Victoria to adults of I. bicolor. Material examined.—**New South Wales**. Dorrigo Nat. Pk., Never Never Picnic Area, 27-28.ix.1986, [may be prepupae present], (ANIC, ~37). **Queensland**. Lamington Nat. Pk., O'Reillys, Border Trail, 920-1000 m, 11.i.1991, under bark, D.A. Pollock & L.A. Reichert, (DAPC, 1). **Tasmania**. 4 km SSE Mt. Rufus, 26-28.i.1980, Lawrence & Weir, (ANIC, 12). **Victoria**. Cumberland Scenic Res., 13 km ESE Marysville, 18.i.1978, under bark, Lawrence & Weir, (ANIC, 1) [coll. in assoc. with several adults of I. bicolor]; Cumberland Scenic Res., nr. Cambarville, 1000 m, 7.xii.1990, under bark dead standing Nothofagus cunninghamii, (DAPC, 3; including 1 exuv. and assoc. adult of I. bicolor); Macquarie Nat. Pk., picnic area ca. 35 km E. Bowral, 200 m, 22.i.1991, under bark rainforest tree, (DAPC, 10); Jct. Lowering Gear Track & Acheron Way, ca. 10 km SSW Marysville, 550 m, 6.xii.1990, under bark Nothofagus or Acacia, D.A. Pollock & L.A. Reichert, (DAPC, 10) [coll. with larvae of type 3]. **LARVAL**

TYPE 2 (Fig. 228).—Intra-urogomphal process distinctly produced; inner urogomphal teeth long, slender. Material examined.—**Tasmania**. SW Tasmania, Lower Gordon R. 42.56S 145.50E 42.54S 145.54E, Howard, Hill..., 12R.600 15.ii.1978, handpicking, (ANIC, 1). **LARVAL TYPE 3** (Fig. 229).—Intra-urogomphal process moderately produced (condition between types 1 & 2); inner urogomphal teeth short, blunt (same as type 1); collected in association with both I. niger and I. bicolor adults. Material examined.—**Tasmania**. Lake St. Clair, 25-27.i.1980, Lawrence & Weir, [ANIC, 14 larvae, 1 pupa, 2 adults (I. bicolor)]; Lake St. Clair, i.1980, (DAPC, 2); 4 km SSE Mt. Rufus, 26-28.i.1980, Lawrence & Weir, (ANIC, ~12)[coll. with larvae of type 1; coll. in assoc. with adults of I. niger]. **Victoria**. Jct. Lowering Gear Track & Acheron Way, ca. 10 km SSW Marysville, 550 m, 6.xii.1990, under bark Nothofagus or Acacia, D.A. Pollock & L.A. Reichert, (DAPC, 8) [coll. with larvae of type 1]. **LARVAL TYPE 4** (Fig. 230).—Intra-urogomphal process distinctly produced (very similar, and possibly conspecific with type 2); inner urogomphal teeth well developed, slender. Material examined.—**Western Australia**. Valley of the Giants, near Nornalup, 27.x.1984, J. & N. Lawrence, (ANIC, 2). **LARVAL TYPE 5** (Fig. 231).—Intra-urogomphal process distinctly produced, truncated apically; inner urogomphal teeth relatively elongate, slender. Material examined.—**Australian Capital Territory**. Wombat Creek, Brindabella Range, 12.iv.1978, under bark near fresh slime mold fruiting body, J.F. Lawrence, (ANIC, 1).

Taxonomic notes.—Five larval types are represented in the material examined. The reared larva belongs to type 1, which is known from Tasmania to southern Queensland. Based on the associated adult, this larval type belongs to I. bicolor Blackburn. Larval type 3, which exhibits a slightly more produced intra-urogomphal process, but with the same short, blunt inner urogomphal teeth as type 1, is known from Tasmania and southern Victoria. Possibly specimens of larval types 1 and 3 are conspecific, because they have been collected together both in Tasmania and Victoria. Adults of both I. niger and I. bicolor have been collected in association with larval type 3.

Larval types 2, 4, and 5 are distinct from types 1 and 3 in that the former have distinctly produced intra-urogomphal processes, and more elongate, slender, inner urogomphal teeth. Larval type 2 was collected at the same locality as an adult matching exactly neither the holotype of I. bicolor nor I. tricolor (although det. as I. tricolor by Lawrence). It is thought that at least two species are represented in the examined larval material; the difference between types 1 and 3, and among types 2, 4, and 5 probably represent intraspecific variation, but until these larval types are reared through to adults, or until adult specimens are collected from Western Australia, this cannot be ascertained definitely.

Natural history

Larvae of Temnopalpus have been collected under bark of a variety of tree taxa, including Nothofagus cunninghamii (Hook. fil.) Oerst., N. moorei (F. Muell.) Krasser (Fagaceae), Eucalyptus spp., and other hardwoods. Collections were made from dead logs in a variety of rainforest types, including cool temperate, warm temperate, and subtropical. Larvae were collected under bark on essentially bare sapwood, and were absent from regions of dead logs containing a large amount of loose, decaying, inner bark material. Specimens were collected under bark of logs also with larvae of Morpholycus and Binburrum, but the individual genera were allotopic, under bark of an individual log. Adults have also been taken under bark, in addition to various types of flight intercept traps.

Lawrence and Britton (1994) stated that adults of Temnopalpus possibly are involved in a mimicry complex with species of Heteromastix Boheman (Cantharidae), some of which are coloured similarly to I. bicolor. This trend towards mimicry is possibly quite widespread within Pilipalpinae, most genera of which have at least one species with aposematic colouration.

Geographical distribution (Figs. 240-242)

Members of this genus are restricted to Australia, and their range extends along the eastern coast from Queensland to Tasmania. Of considerable importance biogeographically is the one record, based on two larvae, from extreme SW Western Australia. This is the only record of an Australian pilipalpine from an area other than in or slightly west of, the Great Dividing Range.

Relationships (Fig. 270)

Both Temnopalpus and Malagaethes are relatively primitive Pilipalpinae. Temnopalpus shares with Malagaethes two characters on the head of adults, indicating a possible adelphotaxon relationship between the two taxa. Both taxa have a slightly developed, supra-antennal crest partially concealing the antennal insertions (character 30). Also, the eye is asymmetrically convex, with the anterior convexity less than that of the posterior aspect of the eye (character 29). If these are true synapomorphies, and not homoplasies, then Temnopalpus + Malagaethes are part of a trichotomy with Pilipalpus, and the remaining genera.

Key to Species of Temnopalpus Based on Adults

1(0). Head black or piceous; pronotum red; elytra piceous to black, in most specimens somewhat lighter than head; legs dark except tarsi paler in some specimens ..... Temnopalpus bicolor Blackburn

Entire body variously piceous to black..... Temnopalpus niger Lea

Temnopalpus bicolor Blackburn

Figs. 113, 129, 134, 191, 240

Temnopalpus bicolor Blackburn 1888: 285. TYPE MATERIAL: HOLOTYPE (BMNH), male(?); labelled: "[red trim 'Type' label] / Temnopalpus bicolor, Blackb". TYPE LOCALITY: Australia, South Australia, Port Lincoln —Lea 1917: 168.—1920: 752.—Csiki 1924: 55.

Temnopalpus tricolor Lea 1920: 751. TYPE MATERIAL: HOLOTYPE (SAMA), female; labelled: "tricolor Lea, Type Waratah / 18829 Temnopalpus tricolor Lea Tasmania [this label with 'TYPE' in red ink along right margin]". TYPE LOCALITY: Australia, Tasmania, Waratah.—Csiki 1924: 55. **NEW SYNONYMY**.

Specific epithet.—From the Latin adjective bicolor, meaning two-coloured, pertaining to the contrast in this species between the piceous head and elytra, and the reddish pronotum.

Diagnosis.—See key to species, above.

Description.—TL 3.6-5.6 mm; GEW 1.1-2.0 mm; head piceous to black (including antennae), except mouthparts somewhat lighter coloured; pronotum red; elytra piceous to black, with or without bluish tint; legs piceous except for tarsi, distinctly lighter (some specimens with legs entirely pale may be teneral).

Geographical distribution (Fig. 240).—Adults of Temnopalpus bicolor have been examined from South Australia and Tasmania to southern New South Wales. Temnopalpus larvae matching those of type 1 were collected in Lamington National Park, southern Queensland.

Material examined.—In addition to the types, I examined 35 specimens, from the following localities: **New South Wales**. Blue Mts, no other data, E.W. Ferguson Collection, (ANIC, 2); Monga State Forest, 1984, L. Masner, ss., Eucalyptus forest, 700 m, on ferns, (CNCI, 1); 28.22S 152.51E Sawpit Ck., 23 km E. of Woodenbong, 22.xi.1983, D.C.F. Rentz & M.S. Harvey, stop 63, (ANIC, 1). **South Australia**. Port Lincoln, no other data, (BMNH, 1); Mt. Lofty Rgs., R. Harvey, on Casurina, (SAMA, 1). **Tasmania**. SW Tasmania, Lower Gordon Rl, 42.56S 145.50E 42.54S 145.54E, ii.1977, Howard, Hill..., H.E.C. Survey 12R.2800, handpicking, (ANIC, 1); Launceston, no date, J. Armstrong,

F.E. Wilson Collection, (MVMA, 2); Waratah, Lea & Carter, (SAMA, 2); Waratah, no other data, (SAMA, 1); 42.38S 146.26E 7 km WNW of Mt. Field West 460 m, 1.ii.1980, Lawrence & Weir, (ANIC, 1); Mt. Field N.P., 8-14.i.1984, L. Masner, MT, (CMNC, 1); 42.44S 146.25E, 4 km SWbyW of Tim Shea, 460 m, 3.ii.1980, Lawrence & Weir, under bark rotten logs, (ANIC, 1). **Victoria**. Cumberland Scenic Reserve, nr. Cambarville, 37.43S 145.53E, ca. 1000 m, 8.xii.1990, under bark of dead standing Nothofagus cunninghamii, D.A. Pollock & L.A. Reichert, (DAPC, 3); Cumberland Scenic Reserve, 13 km ESE Marysville, 18.i.1978, Lawrence & Weir, (ANIC, 3) [one spec. coll. 'under bark rotten logs'; another by 'beating foliage of Nothofagus cunninghamii']; 37.43S 145.41E, Mt. Donna Buang, 1200 m, N. of Warburton, 811, 26.i-11.ii.1987, A. Newton & M. Thayer, wet scler.-Noth. cunn. FMHD #87-219, flight interc. (window) trap, (ANIC, 4); 37.50S 146.12E, 6.1 km ESE of Tanjil Bren, 590 m, 818, 29.i-10.ii.1987, A. Newton & M. Thayer, wet scler. forest FMHD #87-244, flight interc. (window) trap, (ANIC, 1); 37.43S 145.42E, Cement Creek, 670 m, N. of Warburton, 812, 26.i-11.ii.1987, A. Newton & M. Thayer, Euc. regnans-Noth. cunn. under bark large log Euc. regnans, (ANIC, 2); Benalla, Helms, (SAMA, 1); You Yangs, ii.1943, C. Oke, (MVMA, 6); Gisborne, 11.1.1919, G. Lyell, F.E. Wilson Collection, (MVMA, 1).

Temnopalpus niger Lea

Figs. 2, 41-43, 114, 138, 150, 178, 241

Temnopalpus niger Lea 1920: 752. TYPE MATERIAL: HOLOTYPE (SAMA), sex unknown; labelled: "niger Lea, Type King I / [rect. greenish label without writing] / 10940 Temnopalpus niger Lea King Island ['TYPE' in red ink along right margin of label]". TYPE LOCALITY: Australia, King Island.—Csiki 1924: 55.

Specific epithet.—From the Latin adjective niger, meaning black, pertaining to the overall dark colouration of adults of this species.

Diagnosis.—See key to species, above.

Description.—TL 3.5-5.1 mm; GEW 1.1-1.9 mm; head piceous to black (including antennae), except labrum and mouthparts distinctly lighter; pronotum dark piceous, variously lighter in colour than head; elytra piceous; legs and entire venter piceous except for coxae, trochanters and tarsi, lighter, rufous.

Geographical distribution (Fig. 241).—Adult specimens of T. niger are known from Tasmania and southern Victoria. This species is sympatric with T. bicolor on Tasmania and in southern Victoria.

Adult material examined.—In addition to the type, I examined 17 specimens, from the following localities: **Tasmania**. Strahan, 1-18, H.J.C., H.J. Carter Collection, (ANIC, 1); 42.06S 146.10E, Lake St. Clair, 750 m, 25-27.i.1980, Lawrence & Weir, J.F. Lawrence Lot 80-6 Piptoporus, (ANIC, 1); Lake St. Clair 25-27.i.1980, Lawrence & Weir, [collected in assoc. with larvae], (ANIC, 1); 4 km SSE Mt. Rufus, 26-28.i.1980, Lawrence & Weir, (ANIC, 2); King Island, no other data, (SAMA, 1). **Victoria**. 37.43S 145.41E, Mt. Donna Buang, 1200 m, N. of Warburton, 811, 26.i-11.ii.1987, A. Newton & M. Thayer, wet scler.-Noth. cunn. FMHD #87-219, flight interc. (window) trap, (ANIC, 7); 36.57S 147.21E, Bogong N.P., 5.5 km E. Strawberry Saddle, 1450 m, 803, 22.i-13.ii.1987, A. Newton & M. Thayer, wet scler. forest FMHD 87-194 flight interc. (window) trap, (ANIC, 4).

Malagaethes Pollock, gen. nov.

Figs. 3, 139, 151, 192, 244, 270

Type species: Malagaethes lawrencei, sp. nov.

Adult

Diagnosis.—Head with supra-antennal crest partly concealing antennal insertions; pronotal disc convex with evenly rounded lateral margins; basolateral pronotal margins with 2-3 small setigerous tubercles per side; apicale and basale of male genitalia subequal in length (Fig. 139); accessory lobes slender, elongate, with several long apical setae (Fig. 139); median lobe crenulate on apicolateral margins (Fig. 151); distribution: Madagascar.

Description.—Body small, moderately depressed; TL 4.8 mm; GEW 1.2 mm; vestiture conspicuous.

HEAD. Punctation umbilicate, sparse. Frontoclypeal suture indistinct. Eye slightly convex in male (female unknown), ocular margin entire. Antennae (Fig. 3). Antennomeres 4-10 short filiform; antennomere 3 and 4 subequal in length; male 2° setae absent; antennomere 2 filiform. Mandibles (mandibles not dissected from specimen). Maxilla with palpomere 4 moderately cultriform.

PRONOTUM (Fig. 192) subcircular (GPW/PL 1.15), lateral margins widest anterad midlength; disc with lateral margins with small tubercles basally, evenly convex dorsally; posterior pronotal margin slightly emarginate medially; pronotal depressions absent; punctation of pronotal disc uniform, shallowly umbilicate (punctures separated by 1-2 x their diameters); anterior pronotal bead marked by small punctures; posterior pronotal bead present, carinate.

ELYTRA thin, malacoderm-like, without longitudinal ridges or carinae; epipleuron traceable to abdominal sternite 3 or anterad, narrow; primary setae elongate, greater than half length of secondary setae, inserted anterad primary punctures; secondary setae relatively few in number.

MALE GENITALIA (Figs. 139, 151). Apicale subequal in length to basale, slightly emarginate distally; accessory lobes slender, sub-parallel sided, greater than half length of apicale, inserted toward apex of apicale; median lobe relatively slender, very acutely pointed; lateral margins subparallel-sided, to very near apex, with distinct denticulae in apical half.

Generic name

The genus name Malagaethes was formed from a combination of Malagasy (adjectival name of people of Madagascar) and the Greek adjective aethes, meaning unusual, in allusion to both the distribution, and the unusual male genitalia of the holotype.

Natural history

Label data from the single known specimen indicate that the specimen may be a rainforest inhabitant.

Geographical distribution (Fig. 244)

This genus is restricted to Madagascar, and is known only from the type locality of the type species, given below.

Relationships (Fig. 270)

This genus is possibly the adelphotaxon of Temnopalpus. See phylogenetic relationships for Temnopalpus, above.

The male genitalia of Malagaethes lawrencei show some autapomorphic features (not treated phylogenetically here), including the crenulate apicolateral margins of the median lobe (Fig. 151), and the reduced number of relatively elongate setae on the

accessory lobes (Fig. 139). These two character states are absent from other examined taxa of Pilipalpinae and the salpingid group.

Malagaethes lawrencei, sp. nov.
Figs. 3, 139, 151, 192, 244

Type material.—HOLOTYPE (USNM), male; labelled: MADAGASCAR: Prov. Fianarantsoa, 7 km W Ranomafana, 1100 m 1-7 November 1988 W.E. Steiner.

Type locality.—Madagascar, 7 km W. Ranomafana.

Specific epithet.—A Latinized adjectival form of the surname of John F. Lawrence (ANIC), after whom I am pleased to name this species, in recognition of his immeasurable contribution to Coleoptera systematics, and in appreciation for the great help to me in various collaborative projects.

Description.—TL 4.8 mm; GEW 1.2 mm; head and pronotum black; elytra piceous except for longitudinal yellow vitta extended from near humerus to posterad midlength (Fig. 192); ventral body surface piceous to black; labrum and all appendages testaceous, except antennae rufotestaceous. Data about the structural features of this species are given above in the generic description.

Geographical distribution (Fig. 244).—See distribution for genus, given above

Material examined.—Known from the holotype, only. For details, see above.

Genus **Pilipalpus** Fairmaire

Figs. 5, 44-46, 115, 130, 140, 152, 193, 243, 270

Pilipalpus Fairmaire 1876: 384. TYPE SPECIES: Pilipalpus dasytoides Fairmaire 1876 (by monotypy).—Blair 1914: 311.—1928: 12.—Blackwelder 1945: 492.—Abdullah 1964b: 3-4.—1967: 63.—Vulcano and Pereira 1972: 31.—Elgueta D. 1989: 36.

Adult

Taxonomic notes.—Pic (1942) described Copobaenus ater (= Pilipalpus dasytoides Fairm.) and C. maculicollis. Abdullah (1964b) revised the genus and described Pilipalpus darwini from Chiloé, Chile. Upon examination, and very rough treatment of the types of the above two species, Abdullah (1967: 63) declared Pic's names invalid because "the mentioned characters do not serve to distinguish the taxa or to place them in the right genus". I agree that Pic's descriptions were brief and incomplete, but they serve to distinguish the taxa, thus satisfying the requirements of Article 13 of the ICZN (1985). Abdullah's mistake was corrected by Vulcano and Pereira (1972) and Elgueta D. (1989).

Ashworth and Hoganson (1987) mentioned Copobaenus cf. nobilis (Fairmaire and Germain) in a list of Coleoptera collected in southern Chile. Examination of these specimens showed that they were misidentified, and are in fact the maculate form of Pilipalpus dasytoides.

Vulcano & Pereira (1972) presented a taxonomic history of Pilipalpus, and were the first to publish Abdullah's (1967) error in reducing Pic's names to nomina nuda. It is interesting to note that Vulcano & Pereira (1972) include Pilipalpus with the genus Ischalia Pascoe, in subfamily Ischaliinae of Pyrochroidae, as was done earlier by Blackwelder (1945).

Pilipalpus is another genus of Pilipalpinae whose species were separated mainly on colour. It is also a genus of which little material was available for study. As mentioned above, the main feature separating members of P. dasytoides and P. maculicollis was the colour of the pronotum. As usual, Abdullah (1964b) examined only types. For example, one of the characters he used to separate P. dasytoides was the structure of the apex of the median lobe. Upon examining the holotype of P. dasytoides (the only specimen seen

by Abdullah), it was found that the tip of the median lobe was broken, possibly during dissection of the specimen. Other specimens I have examined have the apex of the median lobe exactly as in the P. maculicollis form. Detailed examination of the male genitalia of the two forms revealed no significant difference between them. Two other characters used by Abdullah were the relative lengths of the basal struts on the median lobe, and the shape of the apical antennomere. In the two specimens examined by Abdullah, these characters are diagnostic, but additional material has shown they vary. That leaves the colour of the pronotum as the only character separating the two species. There are several other pilipalpine species, notably in Morpholycus and Binburrum which have at least two colour forms; this appears to be the condition also in P. dasytoides.

Diagnosis.—Antennomeres elongate filiform in both sexes (Fig. 6); pronotal disc with slightly arcuate lateral margins, widest anterad midlength; pronotum mostly impunctate with scattered, erect setae; two longitudinal rows of large, umbilicate punctures on either side of midline of pronotum; elytra with indistinct epipleura; apicale with paired dorsal processes, and ventral plate (Fig. 140); median lobe apically spatulate (Fig. 152); distribution: Chile.

Description.—Body small to medium sized, distinctly depressed; TL 5.2-6.0 mm; GEW 1.4-1.8 mm; vestiture conspicuous.

HEAD. Punctation umbilicate, subconfluent. Frontoclypeal suture arcuate, indistinctly impressed. Eye slightly convex in female, moderately convex in male, ocular margin entire. Antennae (Fig. 6) not sexually dimorphic, antennomeres of equal shape and length in males and females; antennomere 2 filiform, 4-10 short filiform; antennomere 3 and 4 subequal in length; male 2° setae absent. Mandibles (Figs. 44-46). Mandibular mola narrow, widest anteriorly, narrowed posteriorly; lateral margin of mandible evenly arcuate to apex; ventral microtrichial row relatively long, microtrichia long; dorsal mandibular ornamentation absent; apex moderately produced. Maxilla with palpomere 4 moderately to markedly cultriform.

PRONOTUM (Fig. 193). Pronotum subquadrate (GPW/PL 1.32-1.46), lateral margins indistinctly arcuate, subparallel sided in some specimens, widest distinctly anterad midlength; disc with lateral margins evenly arcuate, flat dorsally; posterior pronotal margin truncate; pronotal depressions absent; punctation of pronotal disc non uniform, small punctures laterally, with double row of umbilicate punctures postero-medially; anterior pronotal bead marked by small punctures; posterior pronotal bead present, carinate and marked by small punctures.

ELYTRA (Fig. 115) thin, malacoderm-like, without longitudinal ridges or carinae; epipleuron traceable to abdominal sternite 3 or anterad, narrow; primary setae elongate, greater than half length of secondary setae, inserted anterad primary punctures; secondary setae uniformly distributed among primary setae; primary punctures very small, longitudinally elliptical; microsculpture absent.

MALE GENITALIA (Figs. 140, 152). Aedeagus in repose with tegmen oriented ventrad median lobe; apicale shorter than basale, entire distally, with shelf-like distal portion; accessory lobes slender, curved, greater than half length of apicale, inserted toward base of apicale; median lobe relatively slender, enlarged, subspatulate, lateral margins subparallel-sided, tapered gradually distally, smooth throughout entire length.

FEMALE GENITALIA (Figs. 179-180). Spermathecae short, concealed within ovipositor; bursa copulatrix without external ornamentation.

Relationships (Fig. 270)

Pilipalpus is one of the most structurally aberrant genera in Pilipalpinae, and exhibits a number of autapomorphic characters, most notably in the male genitalia. The entire arrangement of the apicale, basale, and accessory lobes in Pilipalpus is unique among males of Pilipalpinae (Fig. 140). Also, the presence of the double row of large, shallow, umbilicate punctures on the pronotum is autapomorphic for the genus.

Pilipalpus occupies an unresolved position in the reconstructed phylogeny, between Temnopalpus + Malagaethes and the Ranomafana - Morpholycus clade. The discovery of the larval stage of Pilipalpus will provide additional evidence as to its phylogenetic relationships among Pilipalpinae, and may provide further resolution in the reconstructed phylogeny.

Pilipalpus dasytoides Fairmaire

Figs. 5, 44-46, 115, 130, 140, 152, 193, 243

Pilipalpus dasytoides Fairmaire 1876: 384. TYPE MATERIAL: HOLOTYPE (BMNH), male; labelled: "[round BMNH label with red trim] Type / Chili Reed / 430 M / Pilipalpus dasytoides. type. Fairm: / [upside down] F. Bates 81-19 / HOLOTYPE. ♂. Pilipalpus dasytoides Fairmaire, 1876. det. M. Abdullah". TYPE AREA: Chile.—Blair 1928: 12.—Blackwelder 1945: 492.—Abdullah 1964b: 5.—Vulcano & Pereira 1972: 32.—Elgueta D. 1989: 36.

Copobaenus ater Pic 1942: 12. TYPE MATERIAL: HOLOTYPE (MNHN), male; labelled: "Chile Pedilus'/ n. sp. / ater n sp / [illegible handwriting, may state 'was in coll Pic'] / MUSEUM PARIS ♂ 669 M PIC 1899 / Pilipalpus dasytoides Fairmaire, 1876. = Copobaenus ater Pic, 1942. HOLOTYPE, ♂. Det. M. Abdullah / Museum Paris / SYNTYPE". TYPE AREA: Chile.—Abdullah 1967: 63-64.—Abdullah 1969: 339.—Vulcano & Pereira 1972: 32.—Elgueta D. 1989: 36.

Copobaenus maculicollis Pic 1942: 12. TYPE MATERIAL: HOLOTYPE (MNHN), male; labelled: "TYPE / MUSEUM PARIS 668 ♂ M PIC 1899 / Chili / maculicollis n sp / Holotype ♂ of Copobaenus maculicollis Pic NOMEN NUDUM Pilipalpus darwini Abdullah 1964. Det. M. Abdullah. PYROCHROIDAE". TYPE AREA: Chile.—Abdullah 1967: 63-64.—Abdullah 1969: 339.—Vulcano & Pereira 1972: 32.—Elgueta D. 1989: 36. **NEW SYNONYMY**.

Pilipalpus darwini Abdullah 1964b: 8. TYPE MATERIAL: HOLOTYPE (BMNH), male; labelled: "Chiloé I., Chile. C. Darwin. / Darwin Coll. 1885.-119. / 431 ♂ / Chiloé 236 a / HOLOTYPE ♂ Pilipalpus darwini Abdullah". TYPE LOCALITY: Chile, Chiloé Island.—Abdullah 1967: 64.—Vulcano & Pereira 1972: 32.—Elgueta D. 1989: 36. **NEW SYNONYMY**.

Notes on type specimens.—Pic (1942) did not state the number of specimens examined of Copobaenus ater. Two specimens were received from MNHN, both of which bear a SYNTYPE label, but only one of which has a label reading 'ater n sp.' Abdullah (1967: 64) considered the latter specimen to be the holotype, while the other specimen is "another male specimen of this specific name from 'Chile', also in the Paris Museum". Possibly this other specimen was seen by Pic (1942) and should be considered part of the type series for Copobaenus ater.

Specific epithet.—The name dasytoides, based on the generic name Dasytes Payk. (Melyridae), refers to the general resemblance of this species to members of that genus.

Description.—Head black, except for (in maculicollis form) mouthparts, rufous; pronotum entirely black, or orange with medial black spot (as in Fig. 193), situated closer to posterior than anterior margin; elytra piceous to black; venter dark piceous to black, except for trochanters and bases of femora, testaceous; structural features of this species are given in the generic description, above.

Natural history notes.—Such information is generally lacking for Pilipalpus. The available data indicate that the species is found in Valdivian rainforest; collections range from November to January. Specimens have been collected on vegetation of Nothofagus obliqua (Mirb.) Oerst.

Geographical distribution (Fig. 243).—Pilipalpus dasytoides is found between 40 and 43° S, in Región de Los Lagos, Chile.

Material examined.—In addition to types, I examined seven specimens, from the following localities: TYPICAL (dasytoides) FORM. **Osorno or Llanquihue Prov**. P.N. Vincente Perez R., Pta. Huano Olivillo, 14.xi.1971, C. Vivar T, (MNNC, 1). **Valdivia Prov**. Huilo Huilo, site B; 28.xi.1987, gen. veg., ACA, TJF, CRM, (NDSU, 1). ATYPICAL (maculicollis) FORM. **Osorno Prov**. Playa Puyehue, P.N. de Puyehue, site 30, 185 m, 15.xii.1977, Valdivian rainforest, Ashworth, Hoganson, Mooers, (NDSU, 2). **Valdivia Prov**. Neltume, 25-26.xi.1987, on Nothofagus obliqua, ACA, TJF, CRM, (NDSU, 1); Pilmaiquen, site F, 9.i.1988, general vegetation, ACA, TJF, CRM. **Other records**. no data, Colección P. Germain, (MNNC, 2).

Ranomafana Pollock, gen. nov.
Figs. 4, 141, 153, 195, 244, 270

Type species: Ranomafana steineri sp. nov.

Adult

Diagnosis.—Eyes symmetrically convex; antennal insertions completely visible dorsally; pronotal disc with four setigerous tubercles along basolateral margins; male genitalia with spatulate accessory lobes, inserted at apex of non-cleft apicale (Fig. 141); body uniformly rufotestaceous (Fig. 195); distribution: Madagascar.

Description.—Body small, moderately convex; TL 4.1 mm; GEW 1.2 mm; vestiture conspicuous.

HEAD. Punctation umbilicate, subconfluent. Frontoclypeal suture arcuate, distinctly impressed. Eye slightly convex in male (female unknown), ocular margin entire. Antennae (Fig. 4). Antennomere 2 filiform, 4-10 submoniliform; antennomeres 3 and 4 subequal in length; male 2° setae absent. Mandibles (mandibles not dissected from unique specimen). Maxilla with palpomere 4 slightly cultriform, almost subsecuriform

PRONOTUM (Fig. 195) subquadrate (GPW/PL 1.42), lateral margins slightly arcuate, widest posterad midlength; disc with lateral margins with small tubercles basally, flat dorsally; posterior pronotal margin slightly emarginate medially; pronotal depressions absent; punctation of pronotal disc shallowly umbilicate, uniform, punctures confluent; anterior pronotal bead marked by small punctures; posterior pronotal bead present, carinate.

ELYTRA thicker, not malacoderm-like, without longitudinal ridges or carinae; epipleuron traceable to apex of elytron, narrow; primary setae elongate, greater than half length of secondary setae, inserted anterad primary punctures; secondary setae uniformly distributed among primary setae.

MALE GENITALIA (Figs. 141, 153). Aedeagus in repose with tegmen oriented dorsolaterad median lobe; apicale shorter than basale, entire distally; accessory lobes subquadrate, less than half length of apicale, inserted toward apex of apicale; median lobe relatively stout, subacutely pointed, lateral margins subparallel-sided, tapered gradually distally, smooth throughout entire length.

Generic name

This name is a noun of Latin form, indicating a Malagasy place name, and also the type locality for the only known species of the genus.

Geographical Distribution (Fig. 244)

This genus is known only from Madagascar, and only from the type locality of the type species, given below.

Relationships (Fig. 270)

This genus occupies an intermediate position between the more highly derived genera and those that are thought to be more primitive. Based on the phylogenetic analysis, Ranomafana is the adelphotaxon to the Incollogenius - Morpholycus clade. The presence of a complete elytral epipleuron places Ranomafana with the above genera; it retains some primitive characters such as the slightly cultriform apical maxillary palpomere, and the moniliform antennomeres (Fig. 4).

Ranomafana steineri, sp. nov.

Figs. 4, 141, 153, 195, 244

Type material.—HOLOTYPE, (NMNH), male; labelled: "MADAGASCAR: Prov. Fianarantsoa, 7 km W Ranomafana, 1100m 23 Sept.-10 October 1988; C. Kremen / Malaise trap in small clearing, montane rain forest".

Type locality.—Madagascar, 7 km W. Ranomafana

Specific epithet.—A Latinized adjective, based on the surname of Warren Steiner, Jr. (NMNH), who has made many excellent captures during his collecting in Madagascar.

Adult

Description.—TL 4.1 mm; GEW 1.2 mm; body colour uniformly rufotestaceous, somewhat slightly darker on head and pronotum. Data about the structural features of this species are given in the generic description.

Geographical distribution (Fig. 244).—Ranomafana steineri is known only from the type locality: 7 km W Ranomafana, Fianarantsoa Province, Madagascar.

Natural history notes.—Nothing is known about the habits of this species, except that it is probably an inhabitant of madagascan montane rainforest (label data).

Material examined.—Known from the holotype, only. For details, see above.

Genus **Incollogenius** Pic

Figs. 5, 47-49, 142, 154, 181, 194, 244, 270

Incollogenius Pic 1916: 18. TYPE SPECIES: Incollogenius testaceipennis Pic 1916 (by monotypy).—Abdullah 1964a: 242.

Adult

Diagnosis.—Antennomeres submoniliform to short filiform; head and pronotum densely punctate, punctures umbilicate and shallow; pronotal disc with rounded lateral margins, widest near midlength; distribution: Madagascar.

Description.—Body small to medium-sized, moderately convex; TL 5.2-8.7 mm; GEW 1.4-2.4 mm; vestiture conspicuous.

HEAD. Punctation umbilicate, subconfluent. Frontoclypeal suture arcuate, distinctly impressed. Eye slightly to moderately convex in both sexes, ocular margin entire. Antennae (Fig. 5). Antennomere2 moniliform, 4-10 submoniliform, or short filiform; antennomere 3 subequal in length to antennomere 4; male 2° setae absent. Mandibles (Figs. 47-49). Mandibular mola narrow, widest anteriorly, narrowed posteriorly; lateral margin of mandible angulate subapically; ventral microtrichial row relatively long, microtrichia long; dorsal mandibular ornamentation absent; apex moderately produced. Maxilla with palpomere 4 moderately cultriform.

PRONOTUM (Fig. 194). Pronotum subquadrate (GPW/PL 1.29-1.51), basolateral margins straight to slightly arcuate, widest anterad, or near midlength; disc with lateral margins evenly arcuate, flat dorsally; posterior pronotal margin slightly emarginate medially; pronotal depressions absent; punctation of pronotal disc shallowly umbilicate, uniform, punctures confluent; anterior pronotal bead marked by small punctures; posterior pronotal bead present, carinate.

ELYTRA thicker, not malacoderm-like, without longitudinal ridges or carinae; epipleuron traceable to near elytral apex, narrow; primary setae elongate, greater than half length of secondary setae, inserted anterad primary punctures; secondary setae uniformly distributed among primary setae.

MALE GENITALIA (Figs. 142, 154). Aedeagus in repose with tegmen oriented laterad median lobe; apicale subequal in length to basale or shorter than basale, entire distally; accessory lobes slender, sub-parallel sided, greater than length of apicale, inserted toward apex of apicale; median lobe relatively stout, subacutely pointed, lateral margins subparallel-sided, tapered gradually distally, smooth throughout entire length.

FEMALE GENITALIA (Fig. 181). Spermathecae elongate, extended outside of ovipositor; bursa copulatrix without external ornamentation.

Taxonomic notes.—Abdullah (1964a) reviewed the species of Incollogenius, examining only type specimens, which were crudely dissected. Two specimens from NMNH do not match types of any known species; these two specimens may be colour varieties of I. lineatus, but additional recently collected material is needed for comparison and analysis of variation. Abdullah's (1964a) key is based almost entirely on colour pattern of the elytra. The differences in male genitalia between the types of I. testaceipennis and I. lineatus indicate that these two species are distinct, however. Abdullah (1964a) provided descriptions for the three species he recognized, and since additional specimens have not been examined, I have chosen not to repeat his descriptions here. The key to species presented below was taken from Abdullah (1964a), and will undoubtedly need revision once additional specimens become available for study.

Larva

The larval stage of Incollogenius is unknown.

Natural history

Very little is known about this genus, due in part, to the scarcity of collected material. Only several specimens have adequate label data, and these were collected in malaise traps in a rainforest clearing.

Geographical distribution (Fig. 244)

The genus Incollogenius is restricted to Madagascar. Its exact range is unknown because of the few specimens available for study.

Relationships (Fig. 270)

The genus Incollogenius has been considered to be one of the more primitive Pilipalpinae (Abdullah 1964a; Peacock 1982). However, based on characters analyzed here, the genus is most closely related to the more derived genera of Pilipalpinae. Incollogenius is the adelphotaxon to Techmessa - Morpholycus clade. Discovery of the larva would be useful for corroborating the phylogenetic position of Incollogenius within this clade.

Key to Species of Incollogenius Based on adults (from Abdullah 1964a)

1(0). Elytra black, rufous along humeral margin.....I. humeralis Pic
Elytra brown or with black stripes.....2

2(1). Elytra brown; 7th and 8th sterna more deeply emarginate; parameres nearly parallel.....I. testaceipennis Pic
Elytra brown with black stripes along sutural margins and near lateral margins;7th and 8th sterna less deeply emarginate; parameres widely separate at apices .....I. lineatus Pic

Incollogenius lineatus Pic

Incollogenius lineatus Pic 1953: 263. TYPE MATERIAL: LECTOTYPE, (MNHN), male; labelled: "Inst. Scient. Madagascar Mt. Tsaratanana 1500 m. forêt de mousses X - 49 R P/ Incollogenius lineatus n sp / TYPE / le type a la bande discale eloignee de la base / MUSEUM PARIS M PIC 1897 / LECTOTYPE ♂ Incollogenius lineatus Pic # 658 Det. M. Abdullah / [upside down] Paris Dorsal". TYPE LOCALITY: Madagascar, Mt. Tsarantanana.—Abdullah 1964a: 243.

Notes on type specimens.—Pic (1953) mentions that he examined two specimens from his collection. One of the labels on the specimen translated for me by J.J. Menier (MNHN), may indicate that the other specimen was considered by Pic to be more 'typical'. No such specimen was found by Menier in MNHN, and Abdullah (1967) did not find it either. Therefore, Abdullah (1964a) was correct in designating the one specimen available as the lectotype, although according to one of the labels on this specimen, the missing specimen probably would have been preferable as lectotype (or holotype) according to Pic.

Specific epithet.—From the Latin adjective lineatus, meaning of a line; linear, pertaining to the longitudinal elytral vittae of this species.

Diagnosis.—See key to species, above.

Description.—See Abdullah 1964a: 243.

Material examined.—Type material, only. For details, see above.

Incollogenius testaceipennis Pic

Incollogenius testaceipennis Pic 1916: 18. TYPE MATERIAL: HOLOTYPE (MNHN), male; labelled: "type / TYPE / Incollogenius Pic testaceipennis Pic / [illegible label] / MUSEUM PARIS M PIC 1899 / 659 M / HOLOTYPE ♂ Incollogenius testaceipennis Pic. Det. M. Abdullah". TYPE AREA: Madagascar.—Pic 1917: 10.—Abdullah 1964a: 244.

Specific epithet.—From a combination of the Latin adjective testaceous and noun penna, meaning wing, pertaining to the uniform yellow-brown colour of the elytron of this species.

Diagnosis.—See key to species, above.

Description.—See Abdullah (1964a: 244)

Material examined.—Type material, only. For details, see above.

Incollogenius humeralis Pic

Incollogenius humeralis Pic 1917: 10. TYPE MATERIAL: HOLOTYPE (MNHN), female; labelled: "MADAGASCAR TANANARIVE / type / 660 ♀ / TYPE / Incollogenius humeralis Pic / MUSEUM PARIS M. PIC 193 / HOLOTYPE ♀ Incollogenius humeralis Pic, Det. M. Abdullah". TYPE LOCALITY: Madagascar, Tananarive.—Abdullah 1964a: 244.

Specific epithet.—Based on the adjectival form of the Latin noun humerus, meaning shoulder, pertaining to the red patch on the elytral humeri of this species.

Diagnosis.—See key to species, above.

Description.—See Abdullah (1964a: 244)

Other material examined.—In addition to the holotype, I examined three specimens from a single locality: **Prov. Fianarantsoa**, 7 km W. Ranomafana, 900 m; malaise trap in small clearing, montane rainforest, W.E. Steiner, 20-31.i.1990, (NMNH, 1); 1-9.ii.1990, (NMNH, 1); 23-28.ii.1990, (NMNH, 1).

Other Incollogenius material examined.—As noted above, two specimens of Incollogenius from NMNH were examined, neither of which match exactly the types of the three species. The localities are: MADAGASCAR. **Prov. Flanarantsoa**, 7 km W. Ranomafana, 110 m, 22-31.x.1988, W.E. Steiner, malaise trap in small clearing, montane rain forest, (NMNH, 1); same locality and data as above, except 15-24.ix.1988, C. Kremen, (NMNH, 1).

Genus **Techmessa** Bates

Figs. 8, 53-55, 87-88, 117, 145, 157, 196, 245-246, 270

Techmessa F. Bates 1874: 113. TYPE SPECIES: I. concolor Bates 1874 (by subsequent designation).—Broun 1880: 423.—Seidlitz 1920: 726.—Arnett 1950: 224.—Watt 1987: 122.

Adult

Diagnosis.—Antennomeres (Fig. 8) elongate filiform in both sexes; mandible falcate, with indistinct mola (Figs. 53-55); pronotum (Figs. 87-88) narrowest basally, widest anterad midlength; head and pronotum with large, umbilicate punctures (Fig. 87-88); distribution: New Zealand.

Description.—Body small to large, moderately convex; TL 5.2-11.8 mm; GEW 1.4-3.1 mm; vestiture conspicuous.

HEAD. Punctation umbilicate, subconfluent. Frontoclypeal suture arcuate, indistinctly impressed. Eye slightly to moderately convex in both sexes, ocular margin entire. Antennae (Fig. 8) sexually dimorphic, antennomeres slightly more elongate in males; antennomere 2 moniliform, 4-10 elongate filiform; antennomere 3 much shorter than 4; male 2° setae present on antennomeres 4-11. Mandibles (Figs. 53-55). Mandibular mola absent; lateral margin of mandible falcate, markedly arcuate to apex; ventral microtrichial row relatively long, microtrichia long; dorsal mandibular ornamentation absent; apex distinctly produced, scythe-like. Maxilla with palpomere 4 moderately cultriform.

PRONOTUM (Figs. 87-88). Pronotum subquadrate (GPW/PL), lateral margins evenly arcuate, slightly more arcuate anteriorly, widest anterad midlength; disc with lateral margins evenly arcuate, evenly convex dorsally; posterior pronotal margin slightly emarginate medially; pronotal depressions absent; punctation of pronotal disc shallowly umbilicate, punctation sparser medially; anterior and posterior beads marked by small punctures.

ELYTRA (Fig. 117) thicker, not malacoderm-like, without longitudinal ridges or carinae; epipleuron traceable around elytral apex, narrow; primary setae elongate, greater than half length of secondary setae, inserted anterad primary punctures; secondary setae uniformly distributed among primary setae; primary punctures large, subcircular; microsculpture absent.

MALE GENITALIA (Figs. 145, 157). Aedeagus in repose with tegmen oriented dorsad median lobe; apicale longer than basale, entire distally; accessory lobes angular, curved, less than half length of apicale, inserted toward apex of apicale; median lobe relatively slender, subacutely pointed, lateral margins subparallel-sided, tapered gradually distally, smooth throughout entire length.

FEMALE GENITALIA. Spermathecae elongate, extended outside of ovipositor; bursa copulatrix without external ornamentation.

Taxonomic notes.—Arnett (1950: 224) designated I. concolor Bates as the type species of Techmessa; Watt's (1987: 124) designation of I. concolor was therefore unnecessary. Among specimens examined in this study, forms keying to I. telephoroides in Watt (1987) appear all to be females, while those matching Watt's description of I. concolor are all males. Both species have been collected together at the same locality. Possibly this is not coincidental, although Watt (1987: 125) mentions a male (damaged)

paralectotype of I. telephoroides. Much of Watt's (1987) key to species is based upon colour. I have, in list of materials examined, treated I. concolor (body all black), I. telephoroides (body all yellow), and I. sp. (body variously bicoloured). These bicoloured specimens do not correspond exactly with either I. longicollis or I. sp. nov., according to Watt's key and descriptions.

Larva

Methods of association.—Watt (1987: 120) based his determination of the larva of Techmessa on the fact that it did not match any of the other two genera: "if the larva described here as Techmessa does not belong to that genus, it must be that of an unknown adult, which seems highly unlikely". I examined a single larva matching Watt's description and figures.

Diagnosis.—Distribution: New Zealand; stemmata absent; asperities absent but marked by punctulae along anterior margin of S9; urogomphal pits very large, separated by distance less than length of urogomphus; urogomphi comparatively short, lateral margins convergent posteriorly.

Description.—HEAD. Lateral margins evenly arcuate through entire length; stemmata absent; hypostomal rods absent; ratio of antennomere lengths (1:2:3): 1.0:0.7:0.5; antennal sensorium distinctly raised, conical; setae on antennomere 2 generally distributed, of varying lengths; setae on antennomere 3 irregularly distributed in apical half of antennomere; apical antennal seta greater than or equal to 1/2 length of antennomere 3.

THORAX. Parabasal ridges present; spiracular laterotergite not distinctly produced laterally; lateral margins of prothorax slightly divergent anteriorly, with rounded corners; margins of prothorax with three setae at anterolateral corner, 1 seta at posterolateral corner; lateral margins of meso- and metathoracic terga with two elongate setae.

ABDOMEN. Parabasal ridges slightly arcuate; entire urogomphal plate slightly darkly pigmented; punctulae distinct on T9, indistinct on T7-T8; terga with one seta adjacent to spiracle; three lateral marginal setae; segment 8 subequal in length to segment 7; posterolateral angle on T8 smooth, without dentiform process.

UROGOMPHAL PLATE. Anterior corner of T9 smooth, not produced into blunt dentiform process; a/b = 1.84; a/c = 2.06; c/b = 0.89; urogomphi with lateral margins distinctly convergent posteriorly, with several tubercles basally, five elongate and one shorter, setae, apices distinctly upturned near midlength; basolateral flange distinctly produced laterally, with one elongate seta per side; dorsum of plate with 2 small setigerous tubercles arranged obliquely, anterad urogomphal bases; inner urogomphal teeth present, large, curved inwardly; inserted near base of urogomphi; intra-urogomphal projection broad, triangular; urogomphal pits relatively large, oblong, subelliptical, separated by less than, or width of single pit, with more heavily sclerotized dorsal margin; asperities on S9 absent, marked by shallow punctulae; distribution New Zealand.

Natural History

Hudson (1934: 103) stated that "all the species of Techmessa are very active insects, and will speedily mutilate each other, unless promptly placed in the laurel bottle." Hudson (1934) stated that I. concolor was abundant amongst forest growth and general foliage about midsummer, and that I. telephoroides was common at flowers from November to February. Label data indicate that both species have been collected from foliage of Nothofagus and Trifolium L. (Leguminosae).

Geographical distribution (Figs. 245-246)

The genus Techmessa lives only in New Zealand. Techmessa concolor and T. telephoroides are widespread, from Auckland to Southland, while T. longicollis is known only from the Bay of Plenty area (Watt 1987: 125).

Relationships (Fig. 270)

Techmessa is the hypothesized adelphotaxon to the unresolved Exocalopus - Morpholycus clade, and exhibits several unique features in both larval and adult stage. Larvae have no stemmata (character 3), and also have no asperities on S9 (character 23). One of the most striking features of adults, at least of T. concolor, is the structure of the mandible (Figs. 53-55). Techmessa is the only pilipalpine which does not have a distinct mandibular mola (character 18). The long falcate mandible is unique in Pilipalpinae and suggests that this genus may be predaceous.

Key to Species of Techmessa Based on Adults (from Watt 1987)

1(0). Body colour uniformly black 2
Body colour not uniformly black.....3

2(1). Legs and antennae uniformly piceous; aedeagus not greatly broadened in basal half; 5.5-7.6 x 1.5-2.0 mm .....T. concolor Bates
Legs yellow, antennae with yellow patches on basal segments; aedeagus considerably broadened in basal half; 6.0-6.7 x 1.5-1.7 mm .....T. longicollis Broun

3(1). Body colour uniformly yellow-brown; form broad, somewhat depressed; 6.8-12.6 x 1.6-3.5 mm.....T. telephoroides Bates
Head, pronotum and underside dark piceous, elytra yellow-brown; form elongate and convex; 6.1-6.4 X 1.5-1.6 mm; Taupo and Wellington areas..... T. sp. nov.

Techmessa concolor Bates

Figs. 8, 53-55, 87-88, 117, 145, 157, 196, 245

Techmessa concolor Bates 1874: 113. TYPE MATERIAL: HOLOTYPE (BMNH), male, not seen; details given in Watt 1987: 124.

Techmessa attenuata Broun 1893: 1172. TYPE MATERIAL: HOLOTYPE (BMNH), male, not seen; details given in Watt 1987: 124.

Techmessa rugicollis Broun 1910: 52. TYPE MATERIAL: HOLOTYPE (BMNH), male, not seen; details given in Watt 1987: 124-125.

Techmessa unicolor Paulus 1971: 83 (lapsus for T. concolor, according to Watt 1987: 125).

Specific epithet.—From the Latin adjective concolor, meaning of the same colour, pertaining to the uniform black body colour of specimens of (the holotype of) this species.

Diagnosis.—General body colour black; legs and antennae uniformly blackish-brown; aedeagus (basale) relatively slender (Fig. 145).

Geographical distribution (Fig. 245).—According to Watt (1987: 125), T. concolor is widely distributed, from Auckland to Southland. I examined specimens from Taupo to Wellington on North Island and from Nelson to Otago Lakes on South Island.

Material examined.—I examined 19 specimens, from the following localities: **Mid Canterbury**. Banks Peninsula, Prices Valley, 26.xii.1983, L. Masner, ss., (CMNC, 5). **Nelson**. Matai V Nelson, 15.i.1976, A.K. Walker, sweeping Trifolium, (NZAC, 1). **Otago Lakes**. Makaroa [=Makarora?], 21-24.i.1978, S. & J. Peck, malaise Nothofagus for. edge, 330 m, (CNCI, 2). **Rangitikei**. Ohakune, 16.xii.1961, G. Kuschel, (NZAC, 1). **Taupo**. Waituhi Forest, 762 m, 23.i.1977, K.J. Fox, (NZAC, 1; DAPC, 1); same as above, except beating ex trees shrubs, (NZAC, 2; DAPC, 1); Waimarino R., 6.i.1930, Hudson Coll. 665 f

(NMNZ, 1). **Wellington**. Silverstream, 19.xii.1909, A.C. O'Connor, (NZAC, 1; NMNZ, 2); Silverstream, (257), i.1908, (NMNZ, 1).

Techmessa telephoroides Bates

Fig. 246

Techmessa telephoroides Bates 1874: 113. TYPE MATERIAL: HOLOTYPE (BMNH), female; types not examined, details given in Watt 1987: 125.

Techmessa varians Broun 1893: 1173. TYPE MATERIAL: LECTOTYPE (BMNH), female; PARALECTOTYPES (NZAC), female; (BMNH), male; types not examined, details given in Watt 1987: 125.

Specific epithet.—A Latinized adjective, based on a perceived resemblance between this species and the genus Telephorus J.C. Schaeffer (Cantharidae)

Diagnosis.—Body colour uniformly yellowish-brown; form broad, somewhat depressed.

Geographical distribution (Fig. 246).—Techmessa telephoroides is distributed widely, from Auckland to Southland (Watt 1987: 125). Examined specimens were from Taupo to Wellington on North Island, and from Nelson to Southland on South Island.

Material examined.—I examined 20 specimens from the following localities: **Nelson**. Flora Camp, Mt. Arthur, 20.i.1948, R. Forster, (NMNZ, 1); Maitai V Nelson, 15.i.1976, A. K. Walker, sweeping Trifolium, (NZAC, 2). **Otago Lakes**. Bold Peak, Lake Wakatipu, 8.i.1921, Hudson Coll. 274 q (NMNZ, 1). **Rangitikei**. Ohakune, 19.i.1917, A. Castle, (NMNZ, 1). **Southland**. Bluff, no other data, (NMNZ, 1). **Taupo**. Rangataua, i.1921, H.H., (NMNZ, 1); Kaimanawa, Nth. Park, 18.xii.1971, J.S. Dugdale, (DAPC, 1). **Wellington**. Wellington, G.V. Hudson, (NMNZ, 1); Titahi Bay, 1.i.1909, A.C. O'Connor, (NMNZ, 2); Stokes Valley, 4.i.1954, B.A. Holloway, (NMNZ, 1); Kaitoke, (413), 27.xii.1909, (NMNZ, 2); Kaitoke, 28.xii.1902, Hudson Coll. 274 m, (NMNZ, 1); Karori, ii.1902, Hudson Coll. 274 n,p (NMNZ, 2); Korokoro Wellington 29.xii.1923, T. Cockcroft, (NZAC, 1). **Localities not found / mapped**: Oio, 20.i.1936, F. Gardner, (NZAC, 1); Motu River, 25.xi.1928, (NZAC, 1).

Techmessa longicollis Broun

Techmessa longicollis Broun 1903: 70. TYPE MATERIAL: HOLOTYPE (BMNH), male, not seen; details given in Watt 1987: 125.

Specific epithet.—From a combination of the Latin adjective longus, meaning long, and noun collum, meaning neck, in reference to the relatively long pronotum in this species.

Diagnosis.—General body colour uniformly black; legs yellow, antennae with yellow patches on basal segments; aedeagus (basale) relatively broad.

Geographical distribution.—Techmessa longicollis is known only from Bay of Plenty, eastern North Island (Watt 1987: 125).

Material examined.—No specimens of Techmessa were examined which match exactly Watt's definition of T. longicollis.

Genus **Techmessodes** Broun

Figs. 9, 56-58, 91-92, 118, 146, 158, 166-167, 197, 205, 232, 247-248, 270

Techmessodes Broun 1893: 1173. TYPE SPECIES: Techmessodes versicolor Broun 1893 (fixed by Arnett 1950: 224).—Seidlitz 1920: 727.—Watt 1987: 125.

Adult

Diagnosis.—Antennomeres (Fig. 9) elongate filiform in both sexes; head and pronotum with umbilicate punctures (Fig. 92); pronotum widest at or near midlength; eyes slightly emarginate near antennal insertions; tibiae with dimorphic setae; distribution: New Zealand.

Description.—Body small to medium-sized, moderately depressed;TL 4.7-6.6 mm; GEW 1.4-2.3 mm; vestiture conspicuous.

HEAD. Punctation umbilicate, subconfluent. Frontoclypeal suture arcuate, indistinctly impressed. Eye slightly convex in female, moderately convex in male, emarginate near antennal insertion. Antennae (Fig. 9) sexually dimorphic, antennomeres more elongate in males; antennomere 2 moniliform, 4-10 elongate filiform; antennomere 3 shorter than antennomere 4; male 2° setae short, on antennomeres 3-11. Mandibles (Figs. 56-58). Mandibular mola narrow, widest anteriorly, narrowed posteriorly; lateral margin of mandible markedly arcuate to apex; ventral microtrichial row relatively long, microtrichia long; dorsal mandibular ornamentation consisting of microtrichia near base; apex moderately produced. Maxilla with palpomere 4 moderately cultriform.

PRONOTUM (Figs. 91-92). Pronotum subquadrate (GPW/PL 1.11-1.29), lateral margins slightly to moderately arcuate, widest near midlength; disc with lateral margins evenly arcuate, flat dorsally with raised area medially; posterior pronotal margin trisinuate; pronotal depression v-shaped, in posterior half; punctation of pronotal disc shallowly umbilicate, punctation sparser medially; anterior pronotal bead marked by small punctures; posterior pronotal bead present, carinate, or marked by small punctures.

ELYTRA (Fig. 118) thicker, not malacoderm-like, without longitudinal ridges or carinae; epipleuron traceable around elytral apex, narrow; primary setae elongate, greater than half length of secondary setae, inserted anterad primary punctures; secondary setae uniformly distributed among primary setae; primary punctures large, subcircular; microsculpture consisting of slight wrinkling.

MALE GENITALIA (Figs. 146, 158). Aedeagus in repose with tegmen oriented ventrad median lobe; apicale longer than basale, slightly emarginate distally; accessory lobes subquadrate or angular, curved, greater than half length of apicale or less than half length of apicale, inserted toward apex of apicale; median lobe relatively slender, subacutely pointed, lateral margins subparallel-sided, tapered gradually distally, smooth throughout entire length.

FEMALE GENITALIA. Spermathecae elongate, extended outside of ovipositor; bursa copulatrix with external denticulate, annular ornamentation.

Taxonomic notes.—Arnett (1950: 224) fixed the type species of Techmessodes as T. versicolor Broun 1893, but stated the genus was monobasic. Watt (1987: 126) invalidly designated T. picticornis (Broun) as the type species on the basis that it was more common and widely distributed than T. versicolor. Although Arnett (1950) was in error by stating that the genus Techmessodes was monobasic, his type designation of T. versicolor is nonetheless valid.

Larva

Methods of association.—Watt (1987: 126) based his description of the larva of Techmessodes on specimens reared from larva to adult of T. picticornis; specimens identified as T. versicolor were identified as such by the fact that they were collected from Northland, where specimens of the former have never been collected.

Diagnosis.—Tergite 8 darkly pigmented, with punctulae laterally; outer margins of urogomphi parallel or divergent posteriorly (Fig. 232); urogomphal pits small, situated under urogomphi, separated by distance greater than length of urogomphus; distribution: New Zealand.

Description.—HEAD (Fig. 205). Lateral margins arcuate, slightly angulate near midlength; stemmata two per side; hypostomal rods absent; ratio of antennomere lengths

(1:2:3): 0.9:0.9:1.0; antennal sensorium distinctly raised, conical; setae on antennomere 2 sparse, apical only; setae on antennomere 3 relatively sparse, in apical third of antennomere; apical antennal seta greater than or equal to 1/2 length of antennomere 3.

THORAX (Fig. 205). Parabasal ridges present; spiracular laterotergite indistinctly produced laterally; lateral margins of prothorax evenly, slightly divergent anteriorly, slightly emarginate near midlength, with two setae at anterolateral corner, 1 seta at posterolateral corner; lateral margins of meso- and metathoracic terga with two elongate setae.

ABDOMEN. Parabasal ridges present, slightly arcuate; entire urogomphal plate slightly darkly pigmented; punctulae very pronounced on T9 and lateral margins of T8, indistinct on T7; terga with no setae adjacent to spiracle; two lateral marginal setae; segment 8 subequal in length to segment 7; posterolateral angle on T8 smooth, without dentiform process.

UROGOMPHAL PLATE (Fig. 232). Anterior corner of T9 smooth, not produced into blunt dentiform process; a/b = 1.96; a/c = 1.36; c/b = 1.43; lateral margins of urogomphi subparallel to slightly divergent posteriorly, without tubercles, with three elongate and one shorter setae; apices distinctly upturned subapically only; basolateral flange slightly produced laterally, with one elongate seta per side; dorsum with 2-3 small tubercles, anterior tubercle only, setigerous; inner urogomphal teeth present, large, curved inwardly; inserted near midlength of urogomphi; intra-urogomphal projection broad, triangular; urogomphal pits relatively small, subtriangular, separated by about 6 x width of single pit; urogomphal pits with more heavily sclerotized dorsal margin; asperities on S9 distinctly tooth like, not coalesced; distribution New Zealand.

Unassociated larval material examined.—NEW ZEALAND. Mt. Te Aroha Auckland Prov., 762 m. 24.x.1967, J.C. Watt, under bark fallen branches Ixerba brexioides, (NZAC, 6); NN, Cobb Res., 1200 m, 12.i.1966, J.C. Watt, under bark Nothofagus log, (NZAC, 5); Pelorus Bridge, 25.vii.1967, J.C. Watt, ex. Aristotelia serrata, em. 15.ii.1968, reared W67/62, (NZAC, 1).

Natural History

Nothing specific has been published on the way of life of this genus. From label data given above, larvae have been collected under bark of Nothofagus (Fagaceae), Ixerba brexioides A. Cunn. (Brexiaceae), and Aristotelia serrata Oliv. (Elaeocarpaceae). Adults of T. picticornis have been collected in Nothofagus forest.

Geographical distribution (Figs. 247-248)

Techmessodes is endemic to New Zealand. T. picticornis is "widely distributed [in] forested areas, Auckland to Fiordland, most common in northern South Island" (Watt 1987: 126). T. versicolor is known from Northland, Auckland, Bay of Plenty, and the Wellington area. The two species of Techmessodes are apparently allopatric.

Relationships (Fig. 270)

Techmessodes is a component of an unresolved trichotomy, with Exocalopus and (Binburrum + (Cyclodenus + Morpholycus)). Based on the sequence of fragmentation of Gondwanaland (Fig. 273), it is likely that Techmessodes and Exocalopus are adelphotaxa. Unique features of Techmessodes include: eyes emarginate (a reversal of character 24); pronotal depression broadly U-shaped; leg setae dimorphic in colour and size (these latter two characters were not included in the analysis).

Key to Species of Techmessodes Based on Adults (from Watt 1987)

1(0). Pronotum at least 1.3 x broader than long, with a distinct, broadly U-shaped depression; colour black; 4.9-6.8 x 1.6-2.4 mm.....T. picticornis (Broun)

Pronotum at most 1.2 x broader than long, with shallow lateral depressions not linked behind; colour yellow and brown or dark brown; 4.7-5.2 x 1.4-1.8 mm ..... T. versicolor Broun

Techmessodes picticornis (Broun)

Figs. 56-58, 91-92, 118, 146, 158, 197, 247

Techmessa picticornis Broun 1880: 424. TYPE MATERIAL: HOLOTYPE (NZAC), female, not seen; details in Watt 1987: 126.

Techmessa distans Sharp 1882: 87. TYPE MATERIAL: LECTOTYPE (BMNH), male; PARALECTOTYPES (BMNH), 3 males, 4 females; types not seen, details given in Watt 1987: 126.

Specific epithet.—From a combination of the Latin adjective pictus, meaning painted, coloured and noun cornu, meaning horn, i.e. antenna. It is unknown to which particular attribute of the antenna of this species Broun was referring.

Diagnosis.—Pronotum at least 1.3 x broader than long, with a well developed, broadly U-shaped depression; colour uniform piceous to black; median lobe without conspicuous denticulae externally.

Description.—TL 4.9-6.8 mm; GEW 1.6-2.4 mm; eyes in males relatively indistinctly convex, ratio of GPW : GHW ≥ 1.0 in males; ratio of GPW : PL 1.3-1.4; pronotum flat, with deep, U-shaped depression; elytra with distinct microsculpture, more granulate in females; ratio of length apicale : length basale (measured along lateral margin) 1.4; apicale emarginate distally, constricted near midlength; accessory lobes slender, widely separated basally, subangulate and setose along entire length; apicale relatively darkly sclerotized except for region of insertion of accessory lobes (Fig. 146); median lobe slender, gradually and evenly narrowed from base to apex, without large denticulae along external ventral margin (Fig. 158); body uniformly dark piceous to black; tibiae and tarsi only slightly lighter in colour.

Geographical distribution (Fig. 247).—Specimens of T. picticornis were examined from Taranaki to Wellington on North Island, and from Nelson and Buller on South Island.

Material examined.—I examined 19 specimens from the following localities: **Buller**. Capleston, Redmans Ck., 8.xi.1972, J.S. Dugdale, beech forest utilization project, (DAPC, 1); Greymouth, 746, (NMNZ, 1); Capleston, 8.xi.1971, J.C. Watt, beaten at night, beech forest utilization project, (NZAC, 1); Mawhera S.F., 11.xi.1971, J. McBurney, beech forest utilization project, (NZAC, 4); Fletchers Creek, 9.xi.1971, J. McBurney, beating, beech forest utilization project, (NZAC, 2); Canaan, Harwood Hole, Abel Tasman N.P., 22.xii.1983, L. Masner, s.s., Nothofagus forest on limestone, (CNCI, 2). **Nelson**. Dun Mountain, Nelson, 12.i.1947, G. Ramsay. **Taranaki**. Mt. Egmont, i.1923, Hudson Coll. 445 e,g, (NMNZ, 2). **Wellington**. Wellington, G.V. Hudson, (NMNZ, 1); Makara Bush, 12.xii.1922, Hudson Coll. 445 c,d, (NMNZ, 2); Makara Bush, 18.xi.1922, Hudson Coll. 445 b, (NMNZ, 1); Wellington Dist., Kaitoke, 29.ii.1915, A.C. O'Connor (NMNZ, 1). **Locality unknown**. No data, (BPBM, 1).

Techmessodes versicolor Broun

Figs. 9, 166-167, 248

Techmessodes versicolor Broun 1893: 1173. TYPE MATERIAL: LECTOTYPE (BMNH), female; PARALECTOTYPE (BMNH), female; types not examined, details given in Watt 1987: 126.

Techmessodes cephalotes Broun 1910: 53. TYPE MATERIAL: LECTOTYPE (BMNH), male; PARALECTOTYPE (BMNH), male; types not examined, details given in Watt 1987: 126.

Specific epithet.—From the Latin adjective versicolor, meaning of many colours, pertaining to the body colour of the typical form of this species.

Diagnosis.—Pronotum at most 1.2 x broader than long, with indistinct depressions; colour yellow and brown or uniformly dark brown; median lobe with conspicuous denticulae externally.

Description.—TL 4.7-5.2 mm; GEW 1.4-1.8 mm; eyes in males relatively convex, ratio of GPW: GHW < 1.0 in males; ratio of GPW : PL 1.1-1.2; pronotum relatively convex, with at most indistinctly defined, U-shaped depression; elytra without microsculpture in both sexes; ratio of length apicale : length basale (measured along lateral margin) 1.9; apicale not constricted proximad insertion of accessory lobes; accessory lobes short, subquadrate, less than .25 length of apicale; apicale with only very slight emargination apically (Fig. 166); median lobe parallel-sided until near apex, then constricted; ventral, external margin of median lobe with large, basally projecting denticulae (Fig. 167); colour of two forms: body uniformly dark brown with head slightly darker, legs lighter brown; or, head rufopiceous, pronotum red-orange, and elytra piceous.

Geographical distribution (Fig. 248)—The one typical specimen with label data was collected in the Auckland area, while those specimens exhibiting the atypical colour form are all from Wellington, North Island (Watt 1987).

Material examined.—I examined nine specimens from the following localities: **Auckland**. Karamatura Valley, Huia, Waitakarere Range, 22.xi.1989, L.B. O'Brien, (DAPC, 1). **Wellington**. Wellington Area ?, 20.xii.1919, Hudson Coll. 241 e, (NMNZ, 1); Kaitoke, 25.xii.1908, (NMNZ, 1); Porirua, 1.i.1909, Hudson Coll. 241 d, (NMNZ, 1); Karori, 21.xii.1887, Hudson Coll. 241 b,c, (NMNZ, 2); Wiltons Bush, Wellington, 23.xii.1933, Hudson Coll. 241 a, (NMNZ, 1). **Localities unknown**. "533", G.V. Hudson Coll, (NZAC, 2); "2082", T. Broun Collection, [this specimen exhibits typical colouration according to Watt], (NZAC, 1).

Taxonomic notes.—Watt (1987: 126) noted that typical specimens of I. versicolor are known only from Northland, Auckland, and Bay of Plenty. All specimens except two examined for this study are atypical in that the pronotum is dark brown rather than yellow-red; these specimens are all from Wellington, as indicated by Watt. The male genitalia of I. versicolor are unique among Pilipalpinae in the presence of many large denticulae along the external ventral surface of the median lobe. This feature is present neither in I. picticornis nor any other Pilipalpinae.

Genus **Exocalopus** Broun

Figs. 10-11, 59-61, 89-90, 119, 144, 156, 198, 206, 233, 249-250, 270

Exocalopus Broun 1893: 1170. TYPE SPECIES: Exocalopus pectinatus Broun 1893 (by monotypy).—Schenkling 1915: 51.—Seidlitz 1920: 727.—Arnett 1950: 221.—Watt 1987: 126.

Adult

Diagnosis.—Male antennomeres pectinate from antennomere 4 (Fig. 10); elongate subserrate in females (Fig. 11); frons and clypeus separated by distinctly raised, U-shaped carina; head with variously developed impunctate area medially; pronotum more elevated along midline, with lateral depressions; distribution: New Zealand.

Description.—Body small to medium-sized, moderately depressed; TL 4.6- 7.5 mm; GEW 1.4-2.6 mm; vestiture conspicuous.

HEAD. Punctation umbilicate, mostly subconfluent, variously absent medially. Frontoclypeal suture arcuate, raised, carinate. Eye slightly to moderately convex in both sexes, ocular margin entire. Antennae (Figs. 10-11) distinctly sexually dimorphic, antennomeres more pectinate in males; antennomere 2 moniliform, 4-10 serrate in females, pectinate in males; antennomere 3 much shorter than antennomere 4; male 2°

setae short, present on antennomeres 4-11. Mandibles (Figs. 59-61). Mandibular mola narrow, widest anteriorly, narrowed posteriorly; lateral margin of mandible angulate subapically; ventral microtrichial row relatively long, microtrichia long; dorsal mandibular ornamentation consisting of microtrichia near base; apex moderately produced. Maxilla with palpomere 4 markedly cultriform.

PRONOTUM (Figs. 89-90). Pronotum subquadrate (GPW/PL), lateral margins constricted anteriorly and posteriorly, widest at or slightly anterad midlength; disc with lateral margins evenly arcuate, flat dorsally, with raised area medially; posterior pronotal margin trisinuate; pronotal depressions subcircular, in anterior half; punctation of pronotal disc shallowly umbilicate (punctures separated by 1-2 x their diameters), with impunctate areas; anterior and posterior beads carinate.

ELYTRA (Fig. 119) thicker, not malacoderm-like, without longitudinal ridges or carinae; epipleuron traceable around elytral apex, narrow; primary setae elongate, greater than half length of secondary setae, inserted anterad primary punctures; secondary setae uniformly distributed among primary setae; primary punctures relatively large, reniform; microsculpture absent.

MALE GENITALIA (Fig. 144, 156). Aedeagus in repose with tegmen oriented ventrad median lobe; apicale longer than basale, entire distally; accessory lobes angular, curved, greater than half length of apicale, inserted toward apex of apicale; median lobe relatively slender, very acutely pointed, lateral margins subparallel-sided, tapered gradually distally, smooth throughout entire length.

FEMALE GENITALIA. Spermathecae elongate, extended outside of ovipositor; bursa copulatrix without external ornamentation.

Taxonomic notes.—Species discrimination in Exocalopus is based almost entirely on form of punctation. However, Watt (1987: 129) mentions that both species are variable. I was not able to separate consistently adults of Exocalopus according to the key characters in Broun (1903) or Watt (1987). In the "material examined" section, males and females are treated separately but they are not separated as E. pectinatus or E. antennalis. Synonymy of these two names may be required, but this was not done here.

Larva

Method of association.—Watt (1987: 127) stated that larvae were collected under bark together with teneral adults; he mentioned also that the identity of the larva of Exocalopus was confirmed by rearing.

Diagnosis.—Inner urogomphal teeth absent (Fig. 233); T8 distinctly longer than either tergite 7 or 9; anterolateral corner of urogomphal plate developed as dentiform process (Fig. 233); distribution: New Zealand.

Description.—HEAD (Fig. 206). Lateral margins arcuate, slightly angulate near midlength; stemmata two per side; hypostomal rods absent; ratio of antennomere lengths (1:2:3): 0.9:0.9:0.8; antennal sensorium distinctly raised, conical; setae on antennomere 2 sparse, apical only; setae on antennomere 3 relatively sparse, in apical third of antennomere; apical antennal seta greater than or equal to 1/2 length of antennomere 3.

THORAX (Fig. 206). Parabasal ridges present; spiracular laterotergite indistinctly produced laterally; lateral margins of prothorax evenly, slightly divergent anteriorly, slightly emarginate near midlength, with two setae at anterolateral corner, 1 seta at posterolateral corner; lateral margins of meso- and metathoracic terga with one elongate and one shorter seta.

ABDOMEN. Parabasal ridges present, moderately arcuate; entire urogomphal plate uniformly darkly pigmented, T8 slightly lighter; punctulae indistinct on T9 and lateral margins of T8; terga with one seta adjacent to spiracle; three lateral marginal setae; segment 8 1.5 x length of segment 7; posterolateral angle on T8 smooth, without dentiform process.

UROGOMPHAL PLATE (Fig. 233). Anterior corner of T9 produced into blunt dentiform process; a/b = 1.88; a/c = 1.24; c/b = 1.52; lateral margins of urogomphi slightly

convergent posteriorly, with single tubercle near base, with four elongate and one shorter, setae; apices distinctly upturned subapically only; basolateral flange distinctly produced laterally, with two elongate setae per side; dorsum of urogomphal plate with 1 setigerous tubercle on base of urogomphi, 1 seta on urogomphal plate, anterad urogomphal bases; inner urogomphal teeth absent; intra-urogomphal projection narrow, subacutely rounded; urogomphal pits medium size, subcircular, separated by approximately 1.5 x width of single pit, with more heavily sclerotized dorsal margin; asperities on S9 distinctly tooth like, not coalesced; distribution New Zealand.

Larval material examined (Fig. 228).—I examined six larvae from the following localities: Cowan Ridge, 3500', nr. Baton R., Nelson, in wet fumagine fungus on Nothofagus, 6.iii.1966, J.C. Watt, (NZAC, 3); Flora Hut, 3000', Mt. Arthur, Nelson, 12.xi.1969, under dead Nothofagus menziesii bark, (NZAC, 1); Capleston, nr. Reefton, under bark Nothofagus log, 8.xi.1971, J.C. Watt [coll. with adult of E. pectinatus], (NZAC, 2).

Natural History

Hudson (1934) collected adults between approximately 1 000 and 1 300 metres elevation. According to label data, both adults and larvae are associated with Nothofagus, including N. menziesii (Hook. fil.) Oerst. Specimens have been collected from Olearia Moench. (Compositae), and from a Podocarpus L'H´erit. ex Pers. (Podocarpaceae) and Weinmannia L. (Cunoniaceae) forest.

Relationships (Fig. 270)

Exocalopus is among the most highly derived genera of Pilipalpinae, and is part of a trichotomy with Techmessodes and (Binburrum + (Cycloderus + Morpholycus)). Based on geological evidence, it would seem likely that Exocalopus and Techmessodes are adelphotaxa. Unique features of this genus include the highly pectinate male antennomeres (character 22) (Fig. 10), the distinct, carinate frontoclypeal suture, the reniform elytral punctures (Fig. 119), and the absence of inner urogomphal teeth on the larva (character 21) (Fig. 233). Characters 21 and 22 are homoplastic within Pyrochroidae.

Geographical Distribution (Figs. 249-250)

The genus Exocalopus is found only in New Zealand, where its range includes Taupo, Taranaki, Wellington, Nelson, North Canterbury, and Bay of Plenty (Watt 1987). In addition, I examined specimens from Gisborne, Rangitikei (North Island) and Buller, Mid Canterbury, Westland, and Central Otago (South Island).

Key to Species of Exocalopus Based on Adults (from Watt 1987)

1(0). Head in both sexes with a large smooth, shining, raised impunctate area between eyes, with punctures confined to extreme lateral margins beside eyes, and a few discal punctures anteriorly, more numerous in female; also with extensive impunctate areas on pronotum; male antenna as in Fig. 7 [Watt's figure, p. 113]; 5.0-7.3 x 1.7-2.8 mm ..... E. pectinatus Broun

Head with impunctate area much smaller, especially in female; impunctate areas of pronotum also much smaller; male antenna with longer lateral processes; 4.0-5.1 x 1.0-1.9 mm ..... E. antennalis Broun

Exocalopus pectinatus Broun

Exocalopus pectinatus Broun 1893: 1170. TYPE MATERIAL: LECTOTYPE (BMNH), male; PARALECTOTYPE (BMNH), female; types not examined, details given in Watt 1987: 129.

Exocalopus nitidiceps Broun 1910: 53. TYPE MATERIAL: HOLOTYPE (BMNH), female; type not examined, details given in Watt 1987: 129.

Exocalopus antennalis Broun

Exocalopus antennalis Broun 1903: 71. TYPE MATERIAL: LECTOTYPE (BMNH), male; PARALECTOTYPES (BMNH), 2 females; types not examined, details given in Watt 1987: 129.

Adult Exocalopus material examined. I examined 36 specimens from the following localities:

MALES. **Buller**. Canaan, Harwood Hole, Abel Tasman N.P., 22.xii.1983, L. Masner s.s., Nothofagus forest on limestone (CNCI, 1); Nelson lakes N.P., Lake Rotoiti, 19.xii.1983, L. Masner, s.s., (CNCI, 1). **Central Otago**. Garvie Mtns., 4.i.1934, E. Heine, (NMNZ, 1); Capleston, Reefton, 8.ci.1971, J.C. Watt, under bark Nothofagus log, (NZAC, 1). **Gisborne**. Raukumara Range ?, (NMNZ, 1). **Mid Canterbury**. Mt. Peel, i.1913, (NMNZ, 2). **North Canterbury**. Arthur's Pass, 8-11 -1-57, E.S. Gorlay, (DAPC, 1); Arthur's Pass, 900 m, 31.xii.1983, L. Masner, s.s., (ANIC, 2; (CMNC, 10). **Taranaki**. Mt. Egmont, 3-4,000 ft., i.1923, beaten out of shrubs, Hudson Coll. 1279 a,b,c,d, (NMNZ, 4); Mt. Egmont, N.P., 16.xii.1983, L. Masner, s.s., Podocarpus Weinamnnia [sic] forest, (CMNC, 1).

FEMALES. **Buller**. Nelson lakes N.P., Lake Rotoiti, 19.xii.1983, L. Masner, s.s., (CMNC, 1); Canaan, Harwood Hole, Abel Tasman N.P., 22.xii.1983, L. Masner, s.s., Nothofagus forest on limestone (CNCI, 1). **North Canterbury**. Arthur's Pass, 13.i.1933, Hudson Coll. 670 f, (NMNZ, 1). **Nelson**. Mt. Arthur, 2800 ft., 7.i.1925, Hudson Coll. 670 b,e (NMNZ, 2). **Rangitikei**. Mt. Wharite ridge, 5.i.1966, A.V. Spain, from Olearia colensoi foliage (NZAC, 1). **Taranaki**. Dawson Falls, Mt. Egmont, 945 m, 14-20.i.1955, G.W. Ramsay, (NZAC, 1). **Westland**. Otira Gorge, xii.1908, Hudson Coll. 670 c, (NMNZ, 1); Westland N.P., Franz Josef Glacier, 2.i.1984, L. Masner, s.s., (CMNC, 1). **Wellington**. Wellington, G.V. Hudson, (NMNZ, 1). **Locality unknown**. No data, (BPBM, 1).

Binburrum Pollock, gen. nov.

Figs. 7, 50-52, 85-86, 116, 131, 135, 143, 155, 168-172, 182, 199, 204, 216, 222, 236-237, 251-253, 270

Type species: Techmessa ruficollis Champion 1895 (here designated).

Adult

Diagnosis.—Antennomeres (Fig. 7) elongate filiform in both sexes; antennomere 4 shorter than combined lengths of antennomeres 2 and 3; body distinctly parallel sided; distribution: Australia.

Description.—Body small to medium-sized, moderately depressed or moderately convex; TL 3.3-8.4 mm; GEW 0.8-2.4 mm; vestiture conspicuous.

HEAD. Punctation umbilicate, subconfluent. Frontoclypeal suture arcuate, distinctly impressed. Eye slightly convex in female, moderately convex in male, ocular margin entire. Antennae (Fig. 7) sexually dimorphic, antennomeres more elongate in males; antennomere 2 moniliform, 4-10 elongate filiform; antennomere 3 and 4 subequal in length; male 2° setae elongate, present on antennomeres 3-11. Mandibles (Figs. 50-52). Mandibular mola narrow, widest anteriorly, narrowed posteriorly; lateral margin of mandible evenly arcuate to apex; ventral microtrichial row relatively short, microtrichia long; dorsal mandibular ornamentation consisting of microtrichia near base; apex moderately produced. Maxilla with palpomere 4 moderately to markedly cultriform.

PRONOTUM (Figs. 85-86). Pronotum subquadrate (GPW/PL), with short, parallel-sided basal collar, lateral margins variously arcuate, widest near midlength; disc with lateral margins evenly arcuate, or with small tubercles basally, evenly convex dorsally, or with flat, raised area medially; posterior pronotal margin trisinuate; pronotal depressions absent, or

subcircular, near mid-length; punctation of pronotal disc uniform, shallowly umbilicate (punctures separated by 1-2 x their diameters), or shallowly umbilicate, uniform, punctures confluent; anterior and posterior beads present, carinate.

ELYTRA (Figs. 116, 135) thicker, not malacoderm-like, without longitudinal ridges or carinae; epipleuron traceable to near, or around elytral apex, narrow; primary setae elongate, greater than half length of secondary setae, inserted anterad primary punctures; secondary setae uniformly distributed among primary setae; primary punctures large, subcircular; microsculpture absent.

MALE GENITALIA (Figs. 143-155). Aedeagus in repose with tegmen oriented dorsad median lobe; apicale subequal in length to basale, slightly emarginate distally or deeply cleft distally; accessory lobes slender, sub-parallel sided, greater than half length of apicale, inserted toward base of apicale; median lobe relatively slender, blunt, rounded, lateral margins subparallel-sided, tapered gradually distally, smooth throughout entire length.

FEMALE GENITALIA (Fig. 182). Spermathecae elongate, extended outside of ovipositor; bursa copulatrix without external ornamentation.

Generic name

This name is derived from the word 'binburra', an Australian aboriginal word for the southern beech tree (Nothofagus spp.). Larvae and adults of this genus are associated with species of Nothofagus, among other tree taxa.

Taxonomic notes

Watt (1987) excluded B. ruficollis from Techmessa, and also from all other described genera of Pilipalpinae. The characters he used to discriminate between the two genera were relative sizes and setation of antennomeres, shape of pronotum, presence of pronotal depressions, and relative coarseness of elytral punctation.

Larva

Methods of association.—Larvae have not been reared successfully to adults for this genus, although this was attempted. Several collections examined contained larvae and adults together from under bark of individual dead trees, and this was used as a tentative association. Hopefully, the larva will be reared to adult for confirmation of its presumed identity.

Diagnosis.—Spiracular laterotergite distinctly produced (Fig. 204); parabasal ridges present on abdominal tergites, not quite meeting medially; lateral areas of T8 more heavily sclerotized than remainder of tergite; anterior corner of T9 developed into acute process (Fig. 216); posterior angle of ventral extension of T8 developed into spine-like process; urogomphal pits subcircular, widely separated; distribution: Australia.

Description.—HEAD (Fig. 204). Lateral margins straight to arcuate, margins subparallel-sided medially; stemmata two per side; hypostomal rods absent; ratio of antennomere lengths (1:2:3): 0.7:0.9:0.8; antennal sensorium moderately raised, dome-like, subelliptical; setae on antennomere 2 sparse, apical only; setae on antennomere 3 relatively sparse, in apical third of antennomere; apical antennal seta greater than or equal to 1/2 length of antennomere 3.

THORAX (Fig. 204). Parabasal ridges present; spiracular laterotergite distinctly produced laterally; lateral margins of prothorax angulate, posterior margins subparallel, then divergent anteriorly near midlength, with two setae at anterolateral corner, 1 seta at posterolateral corner; lateral margins of meso- and metathoracic terga with two elongate setae, or one elongate seta.

ABDOMEN. Parabasal ridges present, slightly arcuate; lateral margins of T8 and entire urogomphal plate distinctly more darkly pigmented; some specimens with all abdominal tergites darkly pigmented with central lighter area; punctulae very pronounced, present on most tergites, esp. T7-T9; terga with no setae adjacent to spiracle; three lateral

marginal setae, or two lateral marginal setae; segment 8 about 1.25 x length of segment 7; posterolateral angle on T8 produced into blunt dentiform process.

UROGOMPHAL PLATE (Figs. 216, 222, 236-237). Anterior corner of T9 produced into blunt dentiform process; a/b = 2.31; a/c = 1.28; c/b = 1.81; lateral margins of urogomphi slightly but distinctly divergent posteriorly, without tubercles, with four elongate and one shorter, setae; apices distinctly upturned subapically only; basolateral flange distinctly produced laterally, with two elongate setae per side; dorsum of urogomphal plate with several small tubercles on urogomphi; inner urogomphal teeth very small, triangular or medium size, curved inwardly; inserted near midlength of urogomphi, or inserted near, or slightly posterad midlength of urogomphi; intra-urogomphal projection broad, subtruncate posteriorly; urogomphal pits relatively small, subcircular, separated by about 4 x width of single pit, with evenly sclerotized dorsal and ventral margins; asperities on S9 distinctly tooth like, not coalesced.

VARIATION. Very few differences were seen among larvae examined, even between those from north Queensland and Tasmania. Among larvae collected in Victoria, body pigmentation differed distinctly. One larval type was creamy yellow in colour (excluding the head and urogomphal plate), while the other was dark brown to black. These two forms may represent the species B. ruficollis and B. concavifrons. Adults of B. ruficollis were collected in association with the lighter of the two larval types. Therefore, the very dark larva may be associated with B. concavifrons. A single larva from Wollomombi Falls, NSW represents another different species, possibly B. bifoveicollis, based on distribution of adults. The urogomphal plate is narrower and the urogomphi relatively more slender and narrowly separated (Figs. 236-237). This larva also has no or only slightly developed urogomphal pits. The genus Binburrum, therefore, has been coded as having both zero, and two urogomphal pits, in the phylogenetic analysis.

Unassociated larval material examined (Fig. 254).—I examined 68 larvae from the following localities: **New South Wales**. Werrikimbe Nat. Pk., Plateau Beech Picnic Area walking trail, 1060m, 22.xii.1990, D.A. Pollock & L.A. Reichert, under bark of Nothofagus moorei, (DAPC, 2); Macquarie Pass National Park, rain forest walk, 200m, 10 km W. Shellharbour, 22.i.1991, D.A. Pollock & L.A. Reichert, under bark, (DAPC, 6); Barrington Tops, Barrington House, 16.vi.1978, S. and J. Peck, log and bark litter, (ANIC, 1); Dorrigo National Park, Never Never Picnic Area, 27-28.ix.1986, J.F. Lawrence, (ANIC, 15); Wollomombi Falls, 40 km E. Armidale, 1978-1979, R. Noske, (ANIC, 1). **Queensland**. 29 km SE Mareeba, Tinaroo Ck. Rd., 3500', 15.x.1982, J.T. Doyen, (ANIC, 1); 17.06S 145.34E, 3 km WbyS Mt. Haig, 1150 m, 3.iv.1984, A. Calder & T. Weir, (ANIC, 2); Lamington National Park, Binna Burra, 25.iii-4.iv.1985, J. & N. Lawrence, under bark and in rotten wood, (ANIC, 25); 16.36S 145.16E, 1 km S. Mt. Lewis, 950 m, 28.iii.1984, A. Calder & T. Weir, (ANIC, 4); Mt. Glorious, Maiala National Park, 600 m, 4.vii.1978, S. & J. Peck, under bark, (ANIC, 2). **Tasmania**. 4 km SSE Mt. Rufus, 26-28.i.1980, J.F. Lawrence & T. Weir, (DAPC, 3) [this sample with adult of B. ruficollis]. **Victoria**. Jct. Acheron Way and Lowering Gear Track, N. Warburton, 550 m, 6.xii.1990, D.A. Pollock & L.A. Reichert, under bark Nothofagus or Acacia, (DAPC, 6)

Natural History

Nothing has been published about the natural history of Binburrum; such information has been gathered from label data as well as personal field observations. Larvae of Binburrum occur under bark of a variety of hardwood trees, and also Nothofagus, Eucalyptus, etc., from a variety of forest types. Adults have been collected mainly in flight intercept traps, or by general collecting off vegetation. Specific details for individual species are given, below.

Geographical Distribution (Figs. 251-254)

Members of Binburrum are known from along the east coast of Australia, from Queensland to Tasmania. No specimens were examined from west of the Great Dividing Range.

Relationships (Fig. 270)

The genus Binburrum is the adelphotaxon to Cycloderus + Morpholycus. Only character 1, the low, dome-like larval antennal sensorium, unites these three genera. Within Binburrum, several character states are reversed, but not in all the species of the genus.

Key to Species of Binburrum Based on Adults

1(0). Frons with distinct concavity between eyes; lateral margins of pronotal disc variously angulate at maximum width, without tubercles; punctation of head and pronotum deep, coarse, rugose; epipleuron distinct to elytral apex; male apicale very deeply cleft; lobes of apicale pointed distally, extended to near apices of accessory lobes; femora piceous with yellow basal area ..... B. concavifrons Pollock, sp. nov.

Frons without distinct concavity, or with very small fovea between eyes; lateral margins of pronotal disc variously shaped; punctation of head and pronotum relatively shallow, umbilicate; epipleuron not continuous to elytral apex; male apicale various, if cleft deeply, then lobes of apicale rounded distally and not extended to apices of accessory lobes; femora unicolorous individually 2

2(1). Head and pronotum with uniform, contiguous, shallowly umbilicate punctures; pronotum of male relatively broad, subequal in width, or slightly less than GHW; apicale with distinct cleft, in lateral view not deflexed away from accessory lobes (Figs. 169-170) 3

Head and pronotum with punctation various, not as above; pronotum of male relatively narrow, width distinctly less than GHW; apicale not, or only slightly cleft distally, in lateral view distinctly deflexed away from accessory lobes (Figs. 171-172) 4

3(2). Lateral margins of pronotal disc each with several small, setigerous tubercles (in most specimens); elytral punctures large; body entirely black, or with red pronotum; all appendages dark in colour; apicale deeply cleft; median lobe elongate, slender; accessory lobes inserted close together in proximal half of apicale (Fig. 169); distributed in TAS, VIC and s. NSW ..... B. ruficollis (Champion)

Lateral margins of pronotal disc each without tubercles; elytral punctures smaller; basal 2 antennomeres, pronotum, scutellum and other appendages variously reddish; apicale moderately cleft; median lobe short, stout; accessory lobes inserted separated from each other, in distal half of apicale (Fig. 170); distributed in NSW and s. QLD ..... B. bifoveicollis (Lea)

4(2). Punctation of head and pronotum deep, coarse, punctures separated by less than their diameters; elytral punctures large, round; elytra flat dorsally, sloped near apex only; body colour uniformly rufotestaceous; apicale very shallowly cleft distally ..... B. angusticollis Pollock, sp. nov.

Punctation of head and pronotum shallow, finer, punctures separated by at least their diameters; elytral punctures small, longitudinally subelliptical; elytra distinctly sloped near midlength; body colour rufotestaceous except for dark elytral fascia; apicale not cleft distally ..... B. ephippiatum (Wilson)

Binburrum angusticollis Pollock, sp. nov.

Figs. 155, 171, 253

Type material.—HOLOTYPE (ANIC), male; labelled: "28.15S 152.28E The Head, nr Wilsons Peak QLD 13 Oct 1984 I. Naumann and J. Cardale coll". PARATYPE (QDPC), male; labelled: "Mt. Tamborine S.E.Q. ix-x, 1978 (Agard) Pitfall trap in rain forest".

Type locality.—Australia, Queensland, nr. Wilsons Peak.

Specific epithet.—From a combination of the Latin adjective angustus, meaning narrow and noun collum, meaning neck, in reference to the relatively narrow pronotum of the two type specimens.

Diagnosis.—Umbilicate punctation on head and pronotum relatively deep and coarse; epipleuron not distinct to elytral apex; colour uniformly rufotestaceous; GPW distinctly narrower than GHW and width across elytral humeri; apicale (Fig. 171) hoodlike, with only shallow cleft distally; median lobe spatulate apically.

Description.—TL 3.6-3.7 mm; GEW 1.0-1.1 mm. Head. Punctures large, ± contiguous, umbilicate; setae relatively short, except for usual, elongate setae; frontoclypeal suture suggested by vaguely impressed concavity; frons evenly convex; male antennal setae relatively long, length ≥ width of antennomeres, apices distinctly recurved posteriorly. Pronotum. GPW narrower than GHW and width across elytral humeri (male only examined); pronotum slightly wider than long; lateral margins of disc slightly arcuate, subangulate at widest point, near midlength; margins smooth, without tubercles; median line absent; depressions oval, anteriorly divergent, situated near midlength; punctures moderately deep, umbilicate; punctation ± contiguous within depressions, sparser anteriorly and medially; pronotum with basal collar. Elytra. Punctures relatively large, round, smaller toward elytral apex, separated by about their individual diameters; secondary setae in vague suggestion of longitudinal rows; epipleuron narrowed abruptly at ventrite 3 or 4, not present to elytral apex; elytron flat dorsally, sloped toward apex only. Male genitalia (Fig. 171). Apicale slightly shorter than basale, hoodlike, cleft only slightly distally, dorso-apical edge deflexed away from accessory lobes; accessory lobes very narrow, inserted together in proximal half of apicale; median lobe parallel-sided, slightly spatulate distally. Colour. Entire body rufotestaceous, with antennomeres 4-11 infuscated, piceous; head slightly darker than pronotum; basal 1/4 of elytra slightly infuscated in one specimen.

Natural history.—The only information available for B. angusticollis is that one specimen was collected in a pitfall trap within rainforest. The two specimens examined were collected in September and October, which is somewhat earlier in the season compared with most collection records of Binburrum.

Geographical distribution (Fig. 253).—Both specimens of B. angusticollis were collected in SE Queensland.

Material examined.—Type material, only. See above, for details.

Binburrum bifoveicollis (Lea)

Figs. 170, 253

Techmessa bifoveicollis Lea 1917: 292. TYPE MATERIAL: HOLOTYPE (SAMA), female; labelled: "bifoveicollis Lea Type Tambourine / I. 6653 Techmessa bifoveicollis Lea Queensland [this label with 'TYPE' in red ink along right margin] / HOLOTYPE Techmessa bifoveicollis Lea D.A. Pollock 1989". TYPE LOCALITY: Australia, Queensland, Tamborine Mountain.—Watt 1987: 124.

Specific epithet.—From a combination of the Latin bi, meaning two, twice, noun fovea, meaning pit, and noun collum, meaning neck, in reference to the paired pronotal depressions of this, and most other species of Binburrum.

Diagnosis.—Appendages and antennomeres 1 and 2, red; scutellum red; elytral punctation closely spaced, punctures relatively small; tegmen (Fig. 170) with accessory lobes short, inserted laterally on apicale.

Description.—TL 4.2-5.2 mm; GEW 1.4-1.7 mm. Head. Punctures large, ± contiguous, shallowly umbilicate; setae relatively short, except for usual, elongate setae; frontoclypeal suture suggested by vaguely impressed concavity; frons evenly convex; male antennal setae moderately long, length < width of antennomeres, apices distinctly recurved posteriorly. Pronotum. GPW subequal to GHW and width across elytral humeri; pronotum slightly wider than long; disc with lateral margins slightly arcuate, subangulate at widest point, smooth, without tubercles or with slightly developed tubercles; median line absent; depressions oval, anteriorly divergent, vaguely defined; punctures shallow, umbilicate; punctation ± contiguous within depressions, sparser anteriorly and medially; pronotum with basal collar. Elytra. Primary punctures relatively small, round, smaller toward elytral apex, separated by about their individual diameters or less; secondary setae in vague suggestion of longitudinal rows; epipleuron narrowed abruptly at ventrite 3 or 4, not present to elytral apex. Male genitalia (Fig. 270). Apicale slightly longer than basale; apicale not hoodlike, cleft moderately; accessory lobes very narrow, bent laterally near apex, with few short setae; median lobe stout, wide. Colour. Of two forms; most specimens (including type) with head, antennomeres 3-11, elytra piceous to black; basal antennomeres, mouthparts, pronotum, and scutellum red; legs testaceous, hind leg in some specimens darker than other two; one specimen with entire body testaceous except for antennomeres 3-11 and posterior half of elytra piceous.

Natural history.—Label data indicate that B. bifoveicollis may be an inhabitant of wet sclerophyll forest. Specimens have been collected in October and November.

Geographical distribution (Fig. 253).—The geographic range of B. bifoveicollis includes New South Wales, and southern Queensland.

Material examined.—In addition to the type, I examined seven specimens from the following localities: **New South Wales**. Upper Williams R., x.1926, Lea and Wilson, (SAMA, 2) [these records not mapped]; Nambucca Riv., no date, H.J. Carter, (ANIC, 1); N. Gippsland, no date, H.W. Davey, F.E. Wilson Collection, (ANIC, 1) [this record not mapped]; Sydney, no other data, E.W. Ferguson Collection, (ANIC, 1); 3 km N. Lansdowne via Taree, wet sclero. for., 20.ix.1983, G. Williams, (ANIC, 1). **Queensland.** Tambourine, no other data, (SAMA, 1).

Binburrum concavifrons Pollock, sp. nov.

Figs. 50-52, 85-86, 116, 135, 143, 168, 199, 251

Type material.—HOLOTYPE (ANIC), male, labelled: "37.43S 145.41E VIC Mt. Donna Buang, 1200 m N. of Warburton 811 26Jan.-11Feb. 1987 A. Newton & M. Thayer / wet scler.-Noth. cunn. FMHD #87-219 flight interc. (window) trap". ALLOTYPE (ANIC), female, same data as holotype. PARATYPES, 66. 42 males, 7 females (ANIC) with same data as holotype. 2 males, 1 female (ANIC), labelled: "38.39S 143.42E VIC Haines Junct. 525m 1.9km W. on Turton Track 809 25Jan.-8Feb.1987 A. Newton & M. Thayer / wet scler. forest FMHD #87-213 flight interc. (window) trap". 1 male (ANIC), labelled: "36.57S 147.21E VIC Bogong N.P. 5.5km E. Strawberry Saddle 1450m 803 22Jan.-13Feb.1987 A. Newton & M. Thayer / wet scler. forest FMHD 87-194 flight interc. (window) trap". 2 females (ANIC), labelled: "37.41S 145.44 E VIC Acheron Gap, 750m NE of Warburton 813 27 Jan.-9Feb.1987 A. Newton & M. Thayer / Noth. cunn.- Euc. regnans pyrethrin fogging old fungusy logs". 1 male (ANIC), labelled: "37.43S 145.42E VIC Cement Creek, 670m N. of Warburton 812 25Jan.-11Feb.1987 A. Newton & M. Thayer / Euc.regnans - Noth.cunn. FMHD #87-222 flight interc. (window) trap". 1 male, 1 female (ANIC), labelled: "37.43S 145.42E VIC Cement Creek,670m N. of Warburton 814 27Jan.-11Feb.1987 A. Newton & M. Thayer / Euc.regnans - Noth.cunn. pyrethrin fogging old fungusy logs". 4 males, 4 females (ANIC), labelled: "38.43S 143.35E Otway NP

390m Binn Rd. 4.3km N. Cape Horn 808 25Jan.-8Feb.1987 A. Newton & M. Thayer / wet scler.forest FMHD #87-210 flight interc. (window) trap".

Type locality.—Australia, Victoria, Mt. Donna Buang (nr. Warburton).

Specific epithet.—From a combination of the Latin adjective concavus, meaning concave, and noun frons, meaning front, in allusion to the frontal concavity of specimens of the type series.

Diagnosis.—Punctation on head deep, irregular, and rugose; frons with large concavity between eyes; lateral margins of pronotal disc subangulate at widest point; epipleuron distinct around to elytral apex; male tegmen (Fig. 168) with apicale deeply cleft; lateral pieces of apicale elongate, pointed distally.

Description.—TL 4.7-8.6 mm; GEW 1.1-2.2 mm. Head. Punctation deep, coarse, and rugose; all setae long, ± erect; frontoclypeal suture marked by ± distinct groove; area of frons between eyes with depression of various extent; male antennae setae short, bristle-like. Pronotum. Disc moderately convex, with lateral margins sinuate from base to maximum width, evenly and slightly arcuate from maximum width to anterior margin, variously angulate at maximum width; median line and paired depressions indistinct in most specimens; punctation coarse, deep, non-umbilicate; setae long, all ± erect. Elytra. Primary punctures large, round, separated by approximately their own diameters; epipleuron distinct completely to elytral apex, becoming dorsal in orientation; elytron flat, sloped only near apex. Male genitalia (Figs. 143, 155, 168). Apicale and basale subequal in length; apicale cleft proximally to accessory lobes; lobes of apicale pointed distally, overlapping dorsally; accessory lobes elongate, inserted close together in proximal half of apicale; median lobe slender, narrowed gradually to apex. Colour. Of two forms: most specimens with head dorsally black, except for parts of basal 2 antennomeres and clypeus and labrum slightly lighter in colour; ventral mouthparts pale; pronotum red; elytra black; legs dark except for pale, basal patches on femora; several specimens with yellow pronotum and elytra, pronotum slightly darker than elytra.

Natural history.—Adults of B. concavifrons were collected in flight intercept traps, and by insecticidal fogging of old, dead logs. Collections were made from wet sclerophyll forest, as well as Nothofagus cunninghamii - Eucalyptus regnans F. Muell. cool temperate forest, from 390 to 1450 m elevation. Specimens were collected in January and February.

Geographical distribution (Fig. 251).—Binburrum concavifrons is known only from Victoria, where it is found on either side of Melbourne, in the Otway Ranges and in the southern extent of the Great Dividing Range.

Material examined.—Type material, only. See above, for details.

Binburrum ephippiatum (Wilson)

Figs. 172, 253

Techmessa ephippiatum Wilson 1926: 40. TYPE MATERIAL: LECTOTYPE (MVMA) (here selected, right specimen on card with 2 specimens, indicated by 'TY' in red ink) sex unknown, labelled: "Blackall Rgs. Q. Oct. 1920 F.E. Wilson / Techmessa ephippiatum WILSON ['TYPE' in red ink] / 2135 - Type 2136 - Paraty / F.E. Wilson Collection". One PARALECTOTYPE mounted on same card as LECTOTYPE. TYPE LOCALITY: Australia, Queensland, Blackall Ranges.—Watt 1987: 124.

Specific epithet.—From the Latin noun ephippium, meaning saddle, probably in allusion to the dark elytral fascia, analogous to a dark saddle on the otherwise pale elytra.

Diagnosis.—Punctures on head and pronotum shallow, umbilicate; punctures relatively widely spaced; pronotum with sides evenly rounded, distinctly narrower than GHW or width across elytral humeri; elytron with broad, dark fascia, not extended completely to lateral elytral margin; punctures on elytra small, longitudinally ovate; apicale (Fig. 172) hoodlike, not cleft distally.

Description.—TL 3.8-4.2 mm; GEW 1.2 mm. Head. Punctation of head uniform, punctures shallow and umbilicate; frontoclypeal suture marked by slightly impressed, arcuate groove; area of frons between eyes evenly convex to slightly flattened; male antennal setae relatively long, length > maximum widths of antennomeres. Pronotum. GPW less than GHW and width across humeri; pronotum only slightly wider than long; lateral margins of disc smooth, without tubercles, somewhat angulate at widest point, near midlength; median line indistinct; depressions shallow, subcircular; punctures relatively shallow, umbilicate, densest within depressions and sparser anteriorly and medially; pronotum with moderately long basal collar. Elytra. Primary punctures small, longitudinally subelliptical, separated by 2-3 times their own widths; epipleuron narrowed apically and not distinct to elytral apex; elytron not flat dorsally, distinctly sloped in posterior half. Male genitalia (Fig. 172). Apicale longer than basale, hoodlike, not cleft distally; dorso-apical edge of apicale deflexed away from accessory lobes; accessory lobes very narrow, inserted close together in proximal half of apicale; median lobe parallel-sided to apex, apex slightly enlarged, bifid. Colour. Head rufotestaceous, antennomeres 5-11 infuscated; elytron testaceous except for broad piceous fascia; fascia occupying about half of elytral length, with wide margin between it and anterior and posterior elytral margins; fascia separated narrowly from lateral elytral margin; entire ventral surface and legs, rufotestaceous.

Geographical distribution (Fig. 253).—Binburrum ephippiatum is known from southeastern Queensland.

Material examined.—In addition to the types, I examined two specimens from the following localities: **Queensland**. Mt. Glorious, 18.ix.1927, H. Hacker, (QMBA, 1); Mt. Glorious, 6-10.1927, H. Hacker, (QMBA, 1).

Binburrum ruficollis (Champion)

Figs. 7, 131, 169, 182, 252

Techmessa ruficollis Champion 1895: 248. TYPE MATERIAL: HOLOTYPE (BMNH), female, mounted on cardboard plate; labelled: "Hobart, Tasmania J.J. Walker / round BMNH 'Type' label / Techmessa ruficollis, Ch. type / [upside down] Techmessa has longer palpi ?= Pilipalpus Fairm / G.C. Champion Coll. B.M. 1927-409. / HOLOTYPE Techmessa ruficollis Champion". TYPE LOCALITY: Australia, Tasmania, Hobart.—Blackburn 1899: 84.—Champion 1899: 54.—Schenkling 1915: 51.—Lea 1917: 291.—Watt 1987: 124.

Specific epithet.—From the Latin adjective rufus, meaning red, and noun collum, meaning neck, pertaining to the red colour of the pronotum of the type.

Diagnosis.—Punctures on head and pronotum large, shallowly umbilicate, and contiguous; pronotal depressions distinct; lateral margins of pronotal disc with small setigerous tubercles in most specimens; epipleuron narrowed abruptly, not distinct to elytral apex; tegmen (Fig. 169) cleft deeply, lateral lobes of apicale rounded distally.

Description.—TL 4.4-5.9 mm; 1.3-1.8 mm. Head. Punctation coarse, confluent; punctures relatively shallow, umbilicate; frontoclypeal suture suggested by vaguely defined depression; male antennal setae elongate but shorter than distal width of antennomere, distinctly recurved distally; frons between eyes flat or with very small fovea medially. Pronotum. GPW greater than GHW in females and subequal to or slightly less than GHW in males; lateral margins of disc with parallel-sided, basal collar, angulate at widest point, then evenly arcuate to anterior margin; anterad midlength in most specimens with several small, setigerous tubercles along each side; median line indistinct; depressions relatively deep and distinct, subcircular to ovate; punctation relatively shallow, umbilicate and uniformly distributed; pronotal setae adpressed except for usual longer setae. Elytra. Primary punctures very large, round, separated by approximately their own diameters; epipleuron narrowed and indistinct by 3rd or 4th ventrite; elytra flat dorsally,

sloped only near apex. Male genitalia (Fig. 169). Apicale and basale subequal in length; apicale cleft deeply, lateral lobes of apicale rounded distally; accessory lobes inserted together at, or slightly proximad, midlength of apicale, only slightly shorter than apicale; median lobe gradually tapered to near apex, then further narrowed into acute tip, subcylindrical in distal half. Colour. Several forms present; typical (most specimens): head black, pronotum red, elytra piceous to black, not so dark as head in most specimens; pronotum with or without (most specimens) dark patches on depressions; another form uniformly piceous-black; third form coloured typically except elytra testaceous and legs rufopiceous.

Natural history.—Label data on examined specimens of B. ruficollis indicate that specimens were collected in both Eucalyptus and/or Nothofagus forest. The single malaise trap record suggests that flight occurs in January. Specimens have been collected during only January and February.

Geographical distribution (Fig. 252).—Binburrum ruficollis is found on Tasmania, through Victoria, and into southern New South Wales.

Material examined.—In addition to the type, I examined 41 specimens from the following localities: **New South Wales**. Clyde Mtn., 1000 m, s.s., 21.i.1984, L. Masner, (CNCI, 1); Brown Mtn, 50 km W. Bega, 1100 m, s.s., 28.i.1984, L. Masner, (CNCI, 2). **Tasmania**. 41.47 S 145.35 E, 4 km E. Roseberry [=Rosebery], 16.i-1.ii.1983, I.D. Naumann & J.C. Cardale, (ANIC, 1); Rufus Canal, 13.5 km WNW Derwent Br., 800 m, Nothofagus rainforest, 26-28.i.1980, A. Newton & M. Thayer, (ANIC, 1); Waratah, no date, A.M. Lea, (SAMA, 1); 42.13 S 146.01 E, Franklin R., 22.i.1983, I.D. Naumann & J.C. Cardale, (ANIC, 1); Lyell Hwy at Franklin R., 55 km ESE Queenstown, open Eucalyptus forest, 19-20.ii.1980, A. Newton & M. Thayer, (ANIC, 1); 42.10 S 146.08 E, 9 km WSW Derwent Br., ex ethanol, 21.i.1983, I.D. Naumann & J.C. Cardale, (ANIC, 2); Hastings St. Res. nr. Newdegate Cave, 130 m, trapped in floating debris, forest stream, 9.ii.1980, A. Newton & M. Thayer, (ANIC, 1); 10 km S. Hellyer Riv., old Nothofagus forest with Asplenium, 10.i.1984, L. Masner, (CNCI, 1), (CMNC, 5); Mt. Field NP Cpgd, 160 m, Eucalyptus woodld, 31.i-4.ii.1980, A. Newton & M. Thayer, (ANIC, 1); Mt. Field N.P., s.s. [= sweep sample ?], 7.i.1984, L. Masner, (CMNC, 2); Mt. Field N.P., malaise trap, 8-14.i.1984, L. Masner, (CMNC, 1); Mt. Field N.P., Wombat Moor, 1080 m, s.s., 8.i.1984, L. Masner, (CNCI, 1); Mt. Field N.P., Mariette Falls, s.s., 13.i.1984, L. Masner, (CNCI, 1); state record only: (SAMA, 1). **Victoria**. Mt. Donna Buang, 1200 m, Eucalyptus-Nothofagus forest, 11-17.i.1980, A. Newton & M. Thayer, (ANIC, 1); 10 m. E. of Beech Forest, 1.i.1967, Z. Liepa, (ANIC, 1); Beech Forest, 11-19.i.1932, F.E. Wilson, (ANIC, 1); Myer's Ck., nr. Healsville, 3.i.1967, Z. Liepa, (ANIC, 1); 37.43S 145.41E, Mt. Donna Buang, N. of Warburton, 1200 m, 810, 26.i - 11.ii.1987, A. Newton & M. Thayer, wet scler.- Noth. cunn. flight intercept trap (ANIC, 5); 38.39S 143.42E, Haines Junct., 1.9 km W. on Turtons Track, 525 m, 809, 25.i - 8.ii.1987, A. Newton & M. Thayer, wet scler. forest, flight intercept (window) trap, (ANIC, 1); 37.41S 145.44E, Acheron Gap, NE of Warburton, 750 m, 813, 27.i - 9.ii.1987, A. Newton & M. Thayer, Noth. cunn. - Euc. regnans flight interc. (window) trap, (ANIC, 1); Acheron Gap, ca. 15 km NNE Warburton, on Acheron Way, 830 m, 6.xii.1990, D.A Pollock & L.A. Reichert, (DAPC, 1); 38.43S 143.35E, Otway NP, Binn Rd. 4.3 km N. Cape Horn, 390 m, 808, 25.i - 8.ii.1987, A. Newton & M. Thayer, wet scler. forest, flight interc. (window) trap (ANIC, 4); Lorne, no date, C. Oke, (MVMA, 1).

Genus **Cycloderus** Solier

Figs. 12, 62-64, 93-100, 120-124, 132, 147, 159, 183, 201, 207, 217, 225, 255-260, 270

Cycloderus Solier 1851: 252. TYPE SPECIES: Cycloderus rubricollis Solier 1851: 253, t. 21, f. 1 (by monotypy).—Lacordaire 1859: 709.—Gemminger and Harold 1869:

2172.—Schenkling 1915: 21.—Seidlitz 1917: 94.—1920: 726.—Blackwelder 1945: 489.—Arnett 1950: 220.—Spilman 1954: 88.—Elgueta D. 1989: 36.

Pythoplesius Kolbe 1907: 113. TYPE SPECIES: Pythoplesius michaelseni Kolbe 1907: 113 (by monotypy)—Seidlitz 1916: 339.—1917: 94.—1920: 1159.—Blackwelder 1945: 489.—Elgueta D. 1989: 36.—Pollock 1992a: 240.

Adult

Diagnosis.—Antennomeres elongate - filiform in both sexes (Fig. 12); dorsal surface with inconspicuous setae (except in one species); dorsal punctation generally deep and faveolate (e.g. Fig. 98, 100); pronotum with variously developed depressions on either side of midline; colour in most species consisting variously of piceous-black and yellow-red in contrasting areas; size generally large, TL of all specimens examined > 7 mm; distribution: Chile and adjacent Argentina.

Description.—Body medium-sized to large, moderately depressed; TL 7.3-14.1 mm; GEW 1.7-4.0 mm; vestiture conspicuous, or inconspicuous.

HEAD. punctation coarse, variously faveolate. Frontoclypeal suture arcuate, indistinctly impressed. Eye moderately convex in female, markedly convex in male, ocular margin entire. Antennae (Fig. 12) sexually dimorphic, antennomeres more elongate in males; antennomere 2 moniliform, 4-10 very elongate, filiform; antennomeres 3 and 4 subequal in length; male 2° setae elongate, on antennomeres 3-11. Mandibles (Figs. 62-64). Mandibular mola narrow, widest anteriorly, narrowed posteriorly; lateral margin of mandible evenly arcuate to apex; ventral microtrichial row relatively long, microtrichia long; dorsal mandibular ornamentation consisting of microtrichia near base; apex moderately produced. Maxilla with palpomere 4 markedly cultriform; .

PRONOTUM (Figs. 93-100). Pronotum subquadrate to subcircular (GPW/PL 1.00-1.64), with short, parallel-sided basal collar, lateral margins variously arcuate; disc with lateral margins evenly arcuate, flat dorsally with raised area medially; posterior pronotal margin trisinuate; pronotal depressions subcircular or with 2 or 3 separate depressions per side; punctation of pronotal disc faveolate, punctures of non-uniform size and shape; anterior and posterior beads present, carinate.

ELYTRA (Figs. 120-124) thicker, not malacoderm-like, without longitudinal ridges or carinae, or with slightly developed ridges; epipleuron traceable around elytral apex, relatively wide; primary setae elongate, greater than half length of secondary setae, inserted anterad primary punctures, or relatively short, less than half length of secondary setae, shorter than diameter of primary puncture; secondary setae uniformly distributed among primary setae, or relatively few in number; primary punctures very large, subquadrate to subcircular; microsculpture absent, or foliate.

MALE GENITALIA (Figs. 147, 159). Aedeagus in repose with tegmen oriented dorsolaterad median lobe; apicale subequal in length to basale or shorter than basale, slightly emarginate distally; accessory lobes slender, sub-parallel sided, greater than length of apicale, inserted toward apex of apicale; median lobe relatively slender, subacutely pointed, lateral margins subparallel-sided, tapered gradually distally, smooth throughout entire length.

FEMALE GENITALIA (Fig. 183). Spermathecae elongate, extended outside of ovipositor; bursa copulatrix with external, spiniform, annular ornamentation.

Larva

Methods of association.—Jackson (1989) described the larva of C. signaticollis, thus establishing a generic larval association. Also, specimens from MNNC were reared to adults of C. magellanicus. Other un-associated larvae were also used in this study.

Diagnosis.—Urogomphal pits with triangular dorsal process (Fig. 225); abdominal tergites with parabasal ridges meeting at midline; T8 more heavily sclerotized than T1-T7, and with uniform punctulae; distribution: Chile and adjacent Argentina.

Description.—HEAD (Fig. 207). Lateral margins markedly arcuate, angulate near midlength; stemmata two per side; hypostomal rods absent; ratio of antennomere lengths (1:2:3): 1.8:1.7:1.7; antennal sensorium moderately raised, dome-like, subcircular; setae on antennomere 2 generally distributed, with a few longer setae apically; setae on antennomere 3 relatively dense, in apical half of antennomere; apical antennal seta greater than or equal to 1/2 length of antennomere 3.

THORAX (Fig. 207). Parabasal ridges present; spiracular laterotergite not distinctly produced laterally; lateral margins of prothorax evenly, slightly divergent anteriorly, slightly emarginate near midlength, with three setae at anterolateral corner, 1 seta at posterolateral corner; lateral margins of meso- and metathoracic terga with three elongate setae.

ABDOMEN. Parabasal ridges present, slightly arcuate; entire urogomphal plate slightly darkly pigmented; punctulae distinct, uniform on T8, marginal on T7; terga with two setae adjacent to spiracle; three lateral marginal setae; segment 8 from 1.0-1.2 x length of segment 7; posterolateral angle on T8 smooth, without dentiform process.

UROGOMPHAL PLATE (Figs. 217, 225). Anterior corner of T9 smooth, not produced into blunt dentiform process; a/b = 2.21; a/c = 1.24; c/b = 1.79; lateral margins of urogomphi slightly convergent posteriorly, with single tubercle near base, with four elongate and one shorter, setae; apices slightly upturned near apex; basolateral flange slightly produced laterally, with two elongate setae per side; dorsum of urogomphal plate with 2 small setigerous tubercles arranged longitudinally on urogomphi; inner urogomphal teeth large, curved inwardly, inserted near midlength of urogomphi; intra-urogomphal projection broad, triangular; urogomphal pits medium size, oblong, subelliptical, separated by less than, or width of single pit, with more heavily sclerotized dorsal margin; pits with triangular dorsal process (Fig. 225); asperities on S9 not distinctly tooth-like, coalesced.

Taxonomic notes.—Although no structural features were found which separate larvae of Cycloderus, larvae in certain collections had T8 and the urogomphal plate uniformly pigmented, while others had a lighter spot near the urogomphal tubercles. It is not known, however, whether or not this is a significant character for separating species.

Unassociated larval material examined.—I examined 21 larvae from the following localities: **CHILE. Prov. Magallanes**. Rio San Juan, 25.i.1976, T. Cekalovic, (ANIC, 6); Seno Otway, Rio el Ganso, 31.vii.1962, T. Cekalovic, (DKYC, 1); P.N. Torres del Paine, Laguna Lazo, 13.xi.1985, M. Elgueta, ex log of Nothofagus pumilio [reared to adult of C. magellanicus; coll. in association with Mecopselaphus maculicollis Solier (Oedemeridae)], (MNNC, 4). **Prov. Malleco**. 2 km E. Lago Malleco, 1.i.1983, A.F Newton and M.K. Thayer, (DAPC, 2; ANIC, 5). **Prov. Valdivia**. 8 km N. Valdivia, 13.iv.1969, T. Cekalovic, (ANIC, 3).

Natural history

No detailed accounts of the habits of any species of Cycloderus have been published. Data for this section have been taken from labels on specimens, as well as from personal accounts of collectors of specimens. Details are given for each species, below.

Several species of Cycloderus apparently are inhabitants of (Valdivian?) rainforest, while a paratype of C. immaculicollis, sp. nov. was collected in a 'tundra habitat', at 1450m. In contrast, specimens of C. magellanicus Philippi have been collected at nearly sealevel in magellanic Nothofagus forest.

Larvae of Cycloderus occur under bark of dead trees. Documented hosts of species of Cycloderus include Nothofagus pumilio (Poepp. & Endl.) Krasser, N. betuloides (Mirb.) Oerst., and N. dombeyi (Mirb.) Oerst.

Geographical Distribution (Figs. 255-260)

Specimens were examined from Talca Province, Chile (~ 35° S), to Tierra del Fuego (~ 55° S). Although Cycloderus was recorded previously only from Chile,

specimens of C. immaculicollis sp. nov., C. rubricollis, C. signaticollis, and C. magellanicus are known also from adjacent portions of Argentina.

Relationships (Fig. 270)

The genus Cycloderus is adelphotaxon of Morpholycus, both of which form collectively the adelphotaxon of Binburrum. Synapomorphies of Cycloderus + Morpholycus are the faveolate elytral and pronotal punctation (characters 11 and 13), and possibly hypostomal rods in larvae (character 27).

Key to Species of Cycloderus Based on Adults

1. Elytral disc with slightly elevated, longitudinal carina; males with eyes greatly enlarged, distance between eyes subequal to width of one eye.....2
   Elytron without longitudinal carina; males with eyes greatly enlarged, or not.....3
2(1). Pronotum distinctly constricted posteriorly, cordiform; pronotal markings single, longitudinal dark line along midline.....C. planipennis Fairmaire and Germain
   Pronotum indistinctly constricted posteriorly, subquadrate; pronotal markings paired, on either side of midline, convergent anteriorly ..... C. signaticollis Fairmaire and Germain
3(1). Colour of pronotal disc and frons testaceous to rufous, elytra piceous to black; pronotal punctation along midline deep and dense; size generally smaller (TL < 12mm) 4
   Entire dorsal surface concolourous, piceous; pronotal punctation along midline sparse, largely absent near anterior margin; size generally larger (TL > 12mm) ..... C. immaculicollis Pollock, sp. nov.
4(3). Primary elytral setae short, not longer than diameter of primary elytral punctures (Figs. 121-124); elytra with distinct microsculpturing among punctures (Figs. 121-124).....5
   Primary elytral setae long, longer than diameter of primary elytral punctures (Fig. 120); elytra without distinct microsculpturing among punctures (Fig. 120) ..... C. hirsutus Pollock, sp. nov.
5(4). Pronotum more distinctly elevated laterally, lateral areas largely impunctate; pronotal markings variable, confined to median longitudinal area; femora in most specimens with testaceous area of various size; lateral elytral margin in many specimens testaceous .....C. rubricollis Solier
   Pronotum more distinctly elevated medially, lateral areas uniformly punctate; pronotal markings on either side of midline, in some specimens contiguous across midline; femora in most specimens without testaceous areas; lateral elytral margin not testaceous .....C. magellanicus Philippi

Cycloderus immaculicollis Pollock, sp. nov.
Figs. 12, 147, 260

Type material.—Six specimens, three males and two females. HOLOTYPE male (MNNC), labelled: "Argentina Largo [sic] Nahuel Huapi Puerto Blest 26-11-50 / KUSCHEL". ALLOTYPE female (NMNH), labelled: "Puerto Montt Llanquihue Chile Dec 1926 R&E Shannon / CYCLODERUS SP. det T.J. Spilman 1969". Four PARATYPES, one male (NDSU), labelled: "CHILE: Vn. Casablanca P.N. de Puyehue, Osorno Pro. Site 21, El. 1450m, 18-XII-77 Tundra S. of Antillanca Ashworth, Hoganson, Mooers / Not Cycloderus Det. R.H. Arnett, Jr. / Salpingidae sp." One female (MNNC), labelled: "63 / Cycloderus? Kuschel det. 1952 / KUSCHEL". One male (AAAC), labelled: "CHILE, 3700' Pro. OsorNo ANTillaNca 9-II-1968 C.W. OBrieN / ALLEN" [this locality not found / mapped]. One male (NMNH), labelled: "Osorno Chile XII.1977".

Type locality.—Argentina, Neuquén Province, Puerto Blest.

Specific epithet.—From the Latin adjective immaculatus, meaning unstained or unspotted, and noun collum, meaning neck, referring to the non-maculate pronotum of this species.

Diagnosis.—TL of most specimens > 12 mm; body uniformly piceous in colour; pronotum sparsely punctate without lateral tubercles; elytra without microsculpture among non-faveolate punctures.

Description.—TL 11.7 - 14.1 mm; GEW 2.8-4.0 mm. Head. Eyes distinctly sexually dimorphic; eyes of male large, hemispherical; punctation uniform, umbilicate. Pronotum only slightly wider than long; disc with lateral areas somewhat lobate laterad depressions, lateral margins only slightly arcuate anterad short basal collar; median line absent; depressions marked by shallowly depressed, crescentic lateral areas; median area slightly elevated and flat or slightly convex; punctation sparse, individual punctures large but spaced widely, especially anteriorly and laterally; punctures various in size, non-faveolate. Elytra without ridges or microsculpture; primary punctures large, uniform; primary setae ≤ diameter of puncture; secondary setae 3-4 x length of primary setae. Male genitalia (Fig. 147). Tegmen relatively elongate, slender; basale cleft to proximal margin, largely transparent; apicale with shallow basal cleft; accessory lobes elongate, straight; tip of median lobe slender. Colour. Head uniformly rufopiceous in colour; pronotal disc unicolorous, rufopiceous; lateral parts of collar somewhat darker; some specimens with lateral, lobate areas lighter in colour; elytra uniformly rufopiceous, lateral margin of elytra not contrasting in colour.

Natural history.—Few specimens are known of this species, and only one has adequate label data. This specimen was collected at relatively high elevation (1450 m) in a tundra habitat. The Andean tundra, according to Ashworth and Hoganson (1987), consists of grasses, shrubs, and flowering herbs. Clearly, this is different from other species of Cycloderus, which are collected usually in rainforest habitats, at lower elevations.

Geographical distribution (Fig. 260).—Cycloderus immaculicollis has been collected in Chile in Llanquihue and Osorno provinces, and in Argentina, Neuquén province. It is known only from Región de Los Lagos, at approximately 41° S.

Material examined.—Known from the six type specimens. For details, see above.

Cycloderus signaticollis Fairmaire and Germain
Figs. 99-100, 123, 258

Cycloderus signaticollis Fairmaire and Germain 1861: 6. TYPE MATERIAL(MNHN): types not examined. TYPE LOCALITY: Chile, Concepción.—Fairmaire and Germain 1863: 281.—Gemminger & Harold 1869: 1273.—Schenkling 1915: 21.—Seidlitz 1916: 331.—1917: 95.—Blackwelder 1945: 489.—Jackson 1989: 79-83.—Elgueta D. 1989: 36.

Cycloderus binotatus Philippi and Philippi1864: 357. TYPE MATERIAL: HOLOTYPE male (MNNC), labelled: "Typus / Cycloderus binotatus Phil. Holotypus ! ♂ Kuschel det. 1952 / Coleccion Philippi / Chile M.N.H.N. Tipo N° 131". TYPE AREA: Chile, Province Valdivia.—Gemminger & Harold 1869: 1272.—Kolbe 1907: 91.—Schenkling 1915: 21.—Seidlitz 1917: 95.—1920: 1169.—Blackwelder 1945: 489.—Elgueta D. 1989: 36.

Specific epithet.—From the Latin adjective signum, meaning marked and noun collum, meaning neck, in allusion to the characteristic pronotal markings of this species.

Diagnosis.—Eyes of male large, hemispherical; pronotal markings paired, convergent anteriorly, not contiguous across midline; elytra with longitudinal, slightly raised carina; elytral microsculpture among punctures well developed, granulate (Fig. 123).

Description.—TL 11.5 - 13.8 mm; GEW 3.0 - 3.7 mm. Head. Eyes distinctly sexually dimorphic; eyes of male large, hemispherical; punctation deep, faveolate. Pronotum (Figs. 99-100) widest, subangulate, at midlength, with distinct basal collar; lateral margins of disc with several tubercles anterad widest point; pronotal depressions relatively deep, convergent anteriorly; transverse raised area anterad anterior extent of maculations, small depressions anterad raised area; median line evident; punctation faveolate. Elytra (Fig. 123) with longitudinal ridges; microsculpture distinct, granulate; primary punctures relatively large, subquadrate; primary setae adpressed, shorter than diameter of puncture; secondary setae sparse, relatively short, not recurved apically. Male genitalia. Tegmen relatively stout; basale and apicale relatively deeply cleft; accessory lobes elongate, bent near their midlengths; median lobe with moderately slender tip. Colour. Head red dorsally except for area posterad antennal bases; venter of head dark except for paired lighter bands near gula; pronotal maculations paired, convergent anteriorly, extended slightly past midlength; posterior margin dark across entire width; posterolateral pronotal projection infuscate; entire ventral surface of body dark; legs with very indistinct, apical, lighter area, in some specimens; rufous lateral elytral margin absent.

Natural history.—Specimens of C. signaticollis have been collected from foliage of Araucaria Juss. (Araucariaceae), Nothofagus, Chusquea Kunth. (Gramineae), and Myrceugenia Berg. (Myrtaceae). Dates of collection range from November to February, with records of flight from December to February (malaise and flight intercept traps).

Geographical distribution (Fig. 258).—The range of C. signaticollis extends from southern Región del Bío-Bío to Región de Los Lagos in Chile. There is also a single record from Argentina, Neuquén Province.

Material examined.—I examined 23 specimens from the following localities: **ARGENTINA. Neuquén Prov**. Lago Lacar, 21.xii.1987, on Chusquea, ACA, TJF, CRM, (NDSU, 1). **CHILE. Cautín Prov**. Pemehue, colleción P. Germain, (MNNC, 4); 30 km NE Villarrica, 1-30.i.1965, L.E. Peña, (RSMC, 1). **Malleco Prov**. 40 km W. Curcautin, 12.xii.1984, S. & J. Peck, FIT Nothofagus - Araucaria malaise, 1500 m, (CMNC, 1); 40 km W. Angol, Nahuelbuta Nat. Pk., 9.xii.1984-17.ii.1985, S. & J. Peck, FITS, Nothofagus-Araucaria for., 12-1500 m, (CMNC, 2); Nahuelbuta, 6-12.i.1982, Peña, (DAPC, 2); same, 12.i.1982, (DAPC, 1); Nahelbuta Pichinahuel, 1-10.i.1959, L.E. Peña, (RSMC, 4). **Ñuble Prov**. Shangrila, xii.1978, (DAPC, 1) [this locality not mapped]. **Valdivia Prov**. Neltume, 25-26.xi.1987, on Noth. obliqua, ACA, TJF, CRM, (NDSU, 2); Pto. Fuy, site C, 25.xi.1987, gen. vegetation, ACA, TJF, CRM, (NDSU, 1); Pto. Fuy, 25.xi.1987, on Myceugeneila apiculata, ACA, TJF, CRM, (NDSU, 1); Pilmaiquen, site F, 9.i.1988, general vegetation, ACA, TJF, CRM, (NDSU, 1). Country record only: Chili, Reed, (BMNH, 1).

Cycloderus planipennis Fairmaire and Germain

Figs. 97-98, 124, 257

Cycloderus planipennis Fairmaire and Germain 1863: 280. TYPE MATERIAL (MNHN): types not examined. TYPE LOCALITY: Chile, Chillan.—Gemminger & Harold 1869: 2172.—Schenkling 1915: 21.—Seidlitz 1916: 331.—1917: 95.—Blackwelder 1945: 489.—Elgueta D. 1989: 36.

Specific epithet.—From the Latin adjective planus, meaning flat and noun penna, meaning wing, in reference the relatively depressed elytra in this species.

Diagnosis.—Eyes of male large, hemispherical; pronotal markings consisting of single dark stripe along midline, in most specimens attaining anterior margin; elytron with longitudinal ridge; elytral microsculpture distinct (Fig. 124).

Description.—TL 8.4-10.2 mm; GEW 2.3-3.2 mm. Head. Eyes markedly sexually dimorphic; eyes of male large, hemispherical; punctation faveolate. Pronotum (Figs. 97-98) constricted posteriorly, disc with smooth lateral margins; widest anterad middle; depressions simple, subcircular, posterad midlength; punctation relatively fine, uniform,

punctures small, faveolate. Elytra (Fig. 124) with longitudinal ridges; microsculpture distinct, granulate; primary punctures relatively large, subquadrate; primary setae adpressed, shorter than diameter of puncture; secondary setae sparse, relatively short, not recurved apically. Male genitalia. Tegmen moderately slender; basale deeply cleft; apicale shallowly cleft; accessory lobes elongate, slender; apex of median lobe relatively slender. Colour. Dark area on dorsum of head ending posterad antennal bases; venter of head not infuscate in gular region, and extended laterad mouthparts; pronotal maculation central and longitudinal, extended from posterior to anterior margins (more indistinct anteriorly); posterior margin of pronotum infuscate, extended posterolaterally to pronotal angle; posterior pronotal projection infuscate; femora piceous with small testaceous spot near apex; in some specimens, uniformly dark; tibiae darker than femur, almost black.

Geographical distribution (Fig. 257).—The few specimens of C. planipennis examined are all from north of 40° S, in Región del Maule and Región del Bío-Bío.

Material examined.—I examined 11 specimens from the following localities: **CHILE**. **Cautín Prov**. Pemehue, no other data, (MNNC, 2); Pemehue, Germain, no other data, (MNNC, 5). **Ñuble Prov**. Shangrila, xii.1976, (DAPC, 1) [this locality not mapped]; Las Trancas, 19.5 km ESE Recinto, 1250 m, site 647, 10.xii.1982 - 3.i.1983, Newton and Thayer, Nothofagus for., (DAPC, 1). **Talca Prov**. Altos de Vilches, 17/23.xii.1976, G. Arriagada, (MNNC, 2).

Cycloderus hirsutus Pollock, sp. nov.

Figs. 93-94, 120, 259

Type material.—Nine specimens, four males and five females. HOLOTYPE male (NMNH), labelled: "CHILE, Arauco W. Nahuelbuta Caramavida / Pena No. 15 Dec 25-31, 1953 L.E. Pena". ALLOTYPE female (NMNH), labelled: "CHILE, Malleco 30 km.S.E. Curacautin Rio Blanco / Pena No. 55 Feb.1-5, 1959 L.E. Pena". Seven PARATYPES, one male (NMNH), labelled: "CHILE, Arauco Butamalal in jangles el. 1100-1400 M. / Pena No. 18 Jan 23-31, 1954 L.E. Pena". Two females (NMNH), same label data as holotype. One male (NDSU), labelled: "CHILE, Pto. Fui, site C / general vegetation / 7.i.1988; ACA, TJF, CRM". One female (NDSU), labelled: "CHILE, Huilo Huilo, site B / on Amomyrtus luma / 27.xi.1987; ACA, TJF, CRM". One male and one female (RSMC), labelled: "CHILE, Nahuelbuta Pichinahuel 1/10.Enero.1959 L.E. Peña G. colr."

Type locality.—Chile, Arauco Province, Caramavida.

Specific epithet.—From the Latin adjective hirsutus, meaning hairy or shaggy, in reference to the relatively distinct vestiture on the dorsal body surface of adults of this species, compared with other known species of Cycloderus.

Diagnosis.—Dorsal surface with conspicuous, long setae; pronotum reddish, without sharply defined darkened areas (somewhat diffusely piceous areas in some specimens); elytra without longitudinal ridge; elytral microsculpture absent to indistinct (Fig. 120).

Description.—TL 7.4 - 10.8 mm; GEW 1.8 - 3.4 mm. Head. Eyes moderately sexually dimorphic; head punctation coarse, ± faveolate; punctures larger than in signaticollis and planipennis, and with wider interspaces. Pronotum (Figs. 93-94) constricted basally, with distinct collar; lateral margins of disc evenly arcuate anterad collar, without tubercles; median groove indistinct; depressions paired, shallow, indistinctly delimited laterally; median line area of disc elevated only slightly above depressions; pronotal punctures with conspicuous setae. Elytra (Fig. 120) without longitudinal ridges; microsculpture indistinct; primary punctures round, relatively small; primary setae decumbent, longer than diameter of primary punctures; secondary setae relatively dense, elongate, recurved apically. Male genitalia. Tegmen relatively stout; basale deeply cleft; apicale relatively deeply cleft; accessory lobes slender, relatively short; apex of median lobe moderately slender. Colour. Dorsum of head dark except for area between antennal fossae and midlength of eyes; venter of head testaceous between gular sutures;

pronotum yellow/orange, with variously developed, transverse (inverted V) infuscation, darkest medially; lateral regions of collar piceous; venter of thorax and abdomen various, rufous to piceous, never black in specimens examined; legs without light patches;

Natural history.—A single record associates an adult of C. hirsutus with foliage of Amomyrtus luma (Mol.) Legr. and Kaus. (Myrtaceae).

Geographical distribution (Fig. 259).—Cycloderus hirsutus is known from Región de La Araucanía and southern Región de Los Lagos, between 37 and 40° S.

Material examined.—Nine type specimens, only. For details, see above.

Cycloderus rubricollis Solier

Figs. 62-64, 121, 132, 159, 183, 201, 255

Cyclodenus rubricollis Solier 1851: 253, t. 21, f.1. TYPE MATERIAL (MNHN): types not examined. TYPE AREA: Chile.—Lacordaire 1859: 709.—Fairmaire and Germain 1863: 280.—Gemminger & Harold 1869: 2173.—Schenkling 1915: 21.—Seidlitz 1916: 331.—1917: 95.—Blackwelder 1945: 489.—Arnett 1950: 220.—Elgueta D. 1989: 36.

Specific epithet.—From a combination of the Latin adjective rubrum, meaning reddish, and noun collum, meaning neck, in reference to the pronotal colour in this species.

Diagnosis.—Dark pronotal markings absent, or consisting of median spot or short longitudinal band; lateral areas of pronotum variously impunctate; femora with extensive yellow areas; lateral elytral margin yellow in many specimens; elytra without longitudinal ridge; elytral microsculpture indistinct (Fig. 121).

Description.—7.3 - 9.7 mm; GEW 1.7 - 3.2 mm. Head. Eyes only slightly sexually dimorphic; eyes of male only slightly larger than females, non- hemispherical; punctation of head deep, faveolate, without conspicuous setae. Pronotum with short, basal collar; lateral margins of disc evenly arcuate to anterior margin, without distinct tubercles; lateral areas variously impunctate and somewhat elevated; depressions relatively distinct, subcircular; median area elevated. Elytra (Fig. 121) without longitudinal ridges; microsculpture distinct; primary punctures large, subquadrate; primary setae adpressed, shorter than diameter of primary punctures; secondary setae sparse, relatively short. Male genitalia. Tegmen relatively stout; basale moderately deeply cleft; apicale deeply cleft; accessory lobes relatively wide; apex of median lobe relatively broad, straight. Colour. Dark area of dorsum of head in shape of 'V', extended along lateral margins between eyes and antennal fossae; genae and ventral surface of head entirely pale except for band around margin of eye; pronotal markings various; some specimens without defined darker marking; if marking present, then confined to central area, in form of small patch, or short band; posterior margin of pronotum infuscated; ventral surface of body dark, piceous to black, except for pro- and mesocoxae; femora dark basally, with variously developed yellow patch subapically; tibiae with yellow patches; some specimens with narrow yellow, lateral elytral border.

Natural history.—Adults of C. rubricollis have been collected from Valdivian rainforest, Nothofagus-Araucaria forest, and mixed evergreen forest. Specimens have been collected from foliage of Nothofagus dombeyi (Mirb.) Oerst., N. obliqua, Chusquea sp., Drimys winteri (DC) A. Gray (Winteraceae), and Amomyrtus luma. Most collection records are between November and February, but two specimens were collected in April.

Geographical distribution (Fig. 255).—Cycloderus rubricollis is the most widespread species in the genus, and its range in Chile extends from Talca to northern Aisén Province (between 35 and 46° S.). It is also known from Neuquén province, Argentina.

Material examined.—I have examined 81 specimens from the following localities: **ARGENTINA. Neuquén Prov.** Lago Lacar, 21.xii.1987, tree with pointed

needles and purple flowers, ACA, TJF, CRM, (NDSU, 1); same as above, except on Nothofagus, (NDSU, 1). **CHILE. Aisén Prov.** 33 km E Pto. Aisén, Rio Simpson N.P., 30.xii.1984-26.ii.1985, 70 m, FIT, select. cut forest, S.&J. Peck, (CMNC, 4); Q. Andrea, 4.xii.1985, L.E. Peña, (MAIC, 3); (RSMC, 3). **Cautín Prov.** Parq. Nac. Nielol, near Temuco, 14-30.xii.1982, c. 250 m., site 652, native forest, berlesed leaf and log litter, Newton & Thayer (ANIC, 1); 15 km NE Villarrica, Flordel Lago, 14.xii.1984-10.ii.1985, 300 m, FIT, Nothofagus forest, S.&J. Peck, (CMNC, 4); 10 km S Pucon, Vol. Villarrica N.P., 15.xii.1984-10.ii.1985, 900 m, FIT, Nothofagus groveonash [?], S.&J. Peck, (CMNC, 1); 30 km NE Villarrica, 1-30.i.1965, L.e. Peña, (RSMC, 9); Pemehue, no other data, Germain, (MNNC, 10). **Chiloe Prov.** La Velcho, Rio Ventisquero, 5-9.xii.1985, L.E. Peña, (RSMC, 3). **Llanquihue Prov.** Lago Chapo, 13.5 km E. Correntoso, 16-27.xii.1982, 310 m., site 656, Valdivian rainforest, Newton & Thayer (ANIC, 1). **Malleco Prov.** 15 km W. Victoria, 28-30.xii.1976, 200 m., H.F. Howden (ANIC, 1), (CNCI, 1); 6.5 km E. Malalcahuello, 13-31.xii.1982, 1080 m., site 651, N. dombeyi with Chusquea, flight intercept, Newton & Thayer (ANIC, 1); Parque Nac. Tolhuaca, 2 km E. Lago Malleco, 1.i.1983, 925 m., pyrethrin fogging, Nothofagus bark, Newton & Thayer (ANIC, 1); Princesa, 20 km W. Curacautin, 12.xii.1984-16.ii.1985, 1000m, FIT, Nothofagus forest, S.&J. Peck, (CMNC, 2); Puren Contulmo Natur. Mon., 11.xii.1984-13.ii.1985, 350 m, FIT, mixed evergreen forest, S.&J. Peck, (CMNC, 1); 17 km W Angol, 8.xii.1984-16.ii.1986, 800 m, FIT, mixed Nothofagus, S.&J. Peck, (CMNC, 1); Termas Rio Blanco, 1100 m, 23.ii.1979, Valdivian rain forest, on Chusquea sp., Ashworth, Hoganson & Mooers, (NDSU, 1). **Ñuble Prov.** Las Trancas, 19.5 km ESE. Recinto, 10.xii.1982-3.i.1983; 1250 m., site 647, Nothofagus forest, screen sweeping at dusk, Newton & Thayer (DAPC, 2). **Osorno Prov.** Parque Nac. Puyehue, Antillanca Rd., 18-24.xii.1982, 470-720 m., Valdivian rainforest, screen sweeping at dusk, Newton & Thayer (ANIC, 1); Parque Nac. Puyehue, 4.1 km E. Anticura, 19-26.xii.1982, 430 m., site 662, Valdivian rainforest, screen sweeping at dusk, Newton & Thayer (ANIC, 1); Playa Puyehue, P.N. de Puyehue, 185 m., site 30, 22.xii.1977, Valdivian rain forest, on vegetation, Ashworth, Hoganson & Mooers, (NDSU, 2); Laguno Espejo, P.N. de Puyehue, 520 m, site 17, 21.xii.1977, Valdivian rain forest, on Drimys winteri, Ashworth, Hoganson & Mooers, (NDSU, 2); Aguas Callientes, P.N. de Puyehue, 460 m, site 16A, 8.xii.1977, Valdivian rain forest, on vegetation, A.C. Ashworth & J.W. Hoganson, (NDSU, 2); Centinela nr. Pto. Octay, 60m, site 13, 24.xi.1977, on vegetation, Ashworth, Hoganson & Mooers, (NDSU, 1). **Talca Prov.** Altos Vilches, 22.xii.1972, 16/23.xii.1976, G. Arriagada (MNNC, 2); Alto Vilches, 10-12.xii.1976, 1100 m., H.F. Howden (ANIC, 1), (CNCI, 1). **Valdivia Prov.** 4.1 km W. Anticura, 19-25.cii.1982, 270 m., site 663, Valdivian rainforest, flight intercept window/trough trap, Newton & Thayer (ANIC, 1); Valdivia, 8.xii.1982, G. Krahmer (MNNC, 1); 34 km WNW La Union, 17.xii.1984, 700 m, litter mixed evergr. forest, S.&J. Peck, (CMNC, 1). **Localities not found / mapped**: Linares, Fundo Malcho, Cord. Parral, xii.1957, L.E. Peña (Pena No. 35), (NMNH, 4); S. Maule, Tregualemo, 15-23.ii.1959, L.E. Peña (Pena No. 41), (NMNH, 1); Chili, Reed, (BMNH, 5); Chili, C. Darwin, 87-42, (BMNH, 1); R.N., El Bolson, 27.xii.1962, A. Kovacs, (BMNH, 1); Isla Victoria, Monros, 10.i.1943, S.C. de Bariloche, (BMNH, 1).

Cycloderus magellanicus Philippi

Figs. 95-96, 122, 256

Cycloderus magellanicus Philippi 1862: 410. TYPE MATERIAL: LECTOTYPE male (MNNC), labelled: "Magellan / 1131 / Elattoderes maculicollis Blanch. 1853 Kuschel det. 1960". TYPE LOCALITY: Chile, Magallanes.—Philippi & Philippi 1864: 357.—Gemminger & Harold 1869: 2172.—Kolbe 1907: 91.—Schenkling 1915: 21.—Seidlitz 1916: 339.—1917: 95.—1920: 1159.—Blackwelder 1945: 489.—Elgueta D.1989: 36.

Pythoplesius michaelseni Kolbe 1907: 113. TYPE MATERIAL: LECTOTYPE female (ZMHB), labelled: "Punta Arenas Mag. Str. Delfin I. / 97 / V. Seidlitz det. / Pythoplesius magellanicus n. sp. Kolbe / Zool. Mus. Berlin / LECTOTYPE Pythoplesius

michaelseni design. D.A. Pollock 1990". TYPE LOCALITY: Chile, Magallanes, Punta Arenas.—Seidlitz 1916: 339.—1920: 1159.—Blackwelder 1945: 489.—Elgueta D. 1989: 36.—Pollock 1992a: 240.

Taxonomic notes.—In Kolbe's (1907) description of Pythoplesius michaelseni, two different specific epithets were used. This was discussed in Pollock (1992a). In Elgueta D. (1989) the pagination of the description of C. magellanicus is given as Philippi 1862: 112. This apparent error was made first by Blackwelder (1945).

Specific epithet.—Derived from the Latinized name of the southern Chilean region of Magallanes, from which the type specimen was collected.

Diagnosis.—Lateral pronotal margins lobate, well delimited from basal collar (Fig. 95); pronotal markings paired, black, anteriorly convergent; in some specimens, markings contiguous across midline, or with isolated medial spot; elytra without longitudinal carina; elytral microsculpture distinct (Fig. 122).

Description.—TL 7.3 - 10.6 mm; GEW 1.8 - 2.9 mm. Head. Eyes indistinctly sexually dimorphic; eyes of male only slightly larger than those of female; punctation faveolate. Pronotum (Figs. 95-96) with basal collar; lateral margins distinctly arcuate anterad collar, with small tubercles; median line evident; depressions paired, convergent anteriorly; paired raised anterior areas well developed, with slightly elevated ridge extending perpendicular to median line; smaller depression anterad this elevated ridge. Elytra (Fig. 122) without longitudinal ridges; microsculpture distinct; primary punctures large, subquadrate; primary setae adpressed, shorter than diameter of puncture; secondary setae sparse, relatively short, not recurved apically. Male genitalia. Tegmen moderately slender; basale deeply cleft along distal margin; accessory lobes relatively slender, straight. Colour. Dorsum of head dark except for rufous area beginning posterad antennal bases; light area wider than long; venter of head dark except for gula; pronotum red except for posterior bead, and discal infuscations; pronotal markings extending along depressions, across midline anterad middle, down midline a short distance (in most specimens); slight extension across transverse ridge into small anterior depressions; posterolateral pronotal projection dark; entire venter dark; legs concolourous individually; elytral margin dark in all specimens examined

Natural history.—This species is associated with southern magellanic low elevation, Nothofagus pumilio and N. betuloides forest.

Geographical distribution (Fig. 256).—Cycloderus magellanicus is restricted apparently to southern Chile, in the provinces of Magallanes and Osorno. All but one specimen examined are from Región de Magallanes y de la Antartica Chilena, south of 50° S.; the specimen from Osorno Province could possibly have been mislabelled.

Material examined.—In addition to the types, I examined 31 specimens from the following localities: **ARGENTINA**. Tierra del Fuego, Isla Grande, Río Irigoyen, E. side, c. 1 km from seashore, Nothofagus pumilio forest, elev. 10 m, 31.i.1987, J. Niemelä, (NDSU, 1); Tierra del Fuego, Rio McClelland, R. Crawshay, (BMNH, 1); Tierra del Fuego, Rio Grande, Estancia Viamonte, (BMNH, 12). **CHILE. Magallanes Prov**. Laguna Lynch, 28.xii.1968, V. Perez (MNNC, 1) [this locality not found/mapped]; P.N. Torres del Paine Laguna Lazo, 13.xi.1985, M. Elgueta, ex. tronco Nothofagus pumilio en descomposicion nac. laboratorio Dec, 1985 conviendo con Mecopselaphus maculicollis Sol. (Oedemeridae), (MNNC, 1); Punta Arenas, 9-15.i.1966, Flint & Cekalovic, (NMNH, 1); P. Arenas, no other data, (NMNH, 2); Rio Tres Pasos, XII-II-1960, T. Cekalovic, (NMNH, 2); Seno Otway, south part, Nothofagus betuloides & pumilio forest, 170 m, 14.i.1987, J. Niemelä, (NDSU, 1); S. Chile, Rio San Juan, S. Pta. Arenas, 19.xii.1962, P.J. Darlington, (ANIC, 2); Isla Navarino, Puerto Toro, 19.xii.1892, Michaelsen [this locality from Kolbe 1907; specimen not seen]; Isla Lennox, 23.xii.1892, Michaelsen [this locality from Kolbe 1907; specimen not seen]; Magallanes, xii.1929, J.H. Goudie, (BMNH, 3). **Osorno Prov**.

Parque Nac. Puyehue, Antillanca Rd., 18-24.xii.1982, 690 m., Valdivian rainforest, A. Newton & M. Thayer, (ANIC, 2). No data, (BMNH, 2).

Genus **Morpholycus** Lea

Figs. 13-20, 65-67, 101-106, 125-127, 136, 148, 160-165, 184, 200, 208-214, 218-220, 223-224, 226, 261-266, 270

Morpholycus Lea 1917: 287. TYPE SPECIES: Pseudolycus apicalis Macleay 1872 (by subsequent designation).—Blair 1920: 30, 32.—Arnett 1950: 222.—Lawrence 1987: 167.

Adult

Diagnosis.—Antennomeres distinctly serrate or pectinate (Figs. 14-20) [except M. monilicornis, moniliform to subfiliform (Fig. 13)]; generally large size (most specimens with TL > 7 mm); colour combination of orange to red, and black; pronotum with central, longitudinal concavity marked laterally by ridges; posterior pronotal margin trisinuate (Figs. 101, 103, 105); elytra on most specimens with at least suggestions of longitudinal carinae; epipleuron wide, distinct around apex of elytra to sutural margin (Fig. 136); distribution: Australia.

Description.—Body medium-sized to large, distinctly depressed; TL 7.8-13.0 mm; GEW 2.2- 4.0 mm; vestiture conspicuous, or inconspicuous.

HEAD. Punctation coarse, variously faveolate. Frontoclypeal suture arcuate, indistinctly impressed. Eye moderately convex in female, slightly more convex in male, ocular margin entire. Antennae (Figs. 13-20) sexually dimorphic or not, antennomeres more pectinate in males, or of equal shape and length in males and females; antennomere 2 moniliform, 4-10 serrate in females, subpectinate in males, or serrate in both sexes, or moniliform in both sexes; antennomeres 3 and 4 subequal in length; male 2° setae absent. Mandibles (Figs. 65-67). Mandibular mola narrow, widest anteriorly, narrowed posteriorly; lateral margin of mandible evenly arcuate to apex; ventral microtrichial row relatively long, microtrichia long; dorsal mandibular ornamentation consisting of microtrichia near base; apex moderately produced. Maxilla with palpomere 4 moderately to markedly cultriform.

PRONOTUM (Figs. 101-106) subquadrate (GPW/PL 1.15-1.35), lateral margins variously arcuate to parallel-sided; disc with lateral margin evenly arcuate, or with small tubercles basally, flat dorsally with raised area medially; posterior pronotal margin trisinuate; pronotal depressions subcircular or with 2 or 3 separate depressions per side; punctation of pronotal disc faveolate, punctures of non-uniform size and shape; anterior and posterior pronotal beads carinate.

ELYTRA (Figs. 125-127, 136) thicker, not malacoderm-like, with three slightly to distinctly developed, longitudinal carinae; epipleuron traceable around elytral apex, relatively wide; primary setae elongate, greater than half length of secondary setae, inserted anterad primary punctures, or relatively short, less than half length of secondary setae, shorter than diameter of primary puncture; secondary setae uniformly distributed among primary setae, or relatively few in number; primary punctures very large, faveolate, subquadrate to subcircular; microsculpture consisting of slight wrinkling.

MALE GENITALIA (Figs. 148, 160-165). Aedeagus in repose with tegmen oriented ventrad or laterad median lobe; apicale longer than basale, entire distally; accessory lobes subquadrate or angular, curved, less than half length of apicale, inserted toward apex of apicale; median lobe relatively slender, subacutely pointed, lateral margins subparallel-sided, tapered gradually distally, smooth throughout entire length.

FEMALE GENITALIA (Fig. 184). Spermathecae elongate, extended outside of ovipositor; bursa copulatrix without external ornamentation.

Larva

Methods of association.—Mature larvae M. monilicornis, M. costipennis, and M. apicalis were reared successfully to the adult stage. Several collections of larvae (ANIC) of these three species were associated with teneral adults and/or pupae.

Diagnosis.—Distribution: Australia; prothorax widened anteriorly, with anterolateral corners angulate (Fig. 208); T1-T8 with indistinctly developed parabasal ridges; T8 with posterolateral margins more darkly pigmented than rest of tergite; basolateral margins of urogomphal plate variously produced laterally, truncate (Figs. 218-220); single, inner urogomphal tooth on each urogomphus (Figs. 218-220).

Description.—HEAD (Fig. 208). Lateral margins arcuate, slightly angulate near midlength; stemmata two per side; hypostomal rods present, short, posteriorly divergent, or entirely absent; ratio of antennomere lengths (1:2:3): 1.2:1.1:1.0; antennal sensorium slightly raised, dome-like, subelliptical; setae on antennomere 2 generally distributed, with a few longer setae apically; setae on antennomere 3 relatively dense, in apical half of antennomere; apical antennal seta about 1/3 to 1/5 length of antennomere 3.

THORAX (Fig. 208). Parabasal ridges present; spiracular laterotergite not distinctly produced laterally; lateral margins of prothorax angulate, posterior margins subparallel, then divergent anteriorly near midlength, with three setae at anterolateral corner, 1 seta at posterolateral corner; lateral margins of meso- and metathoracic terga with two elongate setae.

ABDOMEN. Parabasal ridges present, moderately arcuate; T8 and urogomphal plate more darkly pigmented; some specimens with lighter region in area of urogomphal tubercles; punctulae indistinct, present mostly marginally only; terga with one or two setae adjacent to spiracle; three lateral marginal setae; segment 8 1.2-1.4 x length of segment 7; posterolateral angle on T8 with or without dentiform process.

UROGOMPHAL PLATE (Figs. 218-220, 223-224, 226). Anterior corner of T9 smooth, not produced into blunt dentiform process; a/b = 2.06-2.65; a/c = 1.27-1.84; c/b = 1.41-2.09; lateral margins of urogomphi subparallel, distinctly convergent posteriorly, or slightly divergent posteriorly, with single tubercle near base; four elongate and one shorter, setae; apices upturned slightly near apex; basolateral flange distinctly produced laterally or indistinct, with two elongate setae per side; dorsum of urogomphal plate with 2 small setigerous tubercles on base of urogomphi, or [M. monilicornis (Fig. 218)] complete transverse row of small non-setigerous tubercles across urogomphal plate near posterior margin; inner urogomphal teeth present, large, curved inwardly, inserted near base or midlength of urogomphi; intra-urogomphal projection acutely pointed, bluntly rounded, or subtruncate posteriorly; urogomphal pits of various size, oblong, subelliptical, separated by 1-5 x width of single pit, with more heavily sclerotized dorsal margin; asperities on S9 not distinctly tooth-like, coalesced; distribution Australia.

Taxonomic notes.—The shape of the urogomphal plate of larvae of M. monilicornis (Fig. 218) and M. costipennis (Fig. 219) is distinctive. Reared larvae of M. apicalis (Fig. 220) are very similar in appearance to four larvae collected in association with adults of M. nigripennis and M. concolor in northern Queensland. Since these larvae were not reared, their exact association is uncertain. The outer urogomphal plate projection in typical larvae of M. apicalis is more or less truncate, with a slight posterior lobe (Fig. 220). The projection in the four larvae from north Queensland has a small lobe in the anterior half of the projection.

Based on close similarity of adults of the north Queensland endemic species M. nigripennis, M. concolor, and M. flabellicornis, it might be expected that their larvae would exhibit comparable similarity. Thus these four specimens could belong to any of these species. Several collections of larvae of the typical "apicalis" form were made from northern Queensland, none of which were collected with adults. Adults of M. flabellicornis are distinctive structurally, while adults of M. concolor and M. nigripennis are separated mainly on colour. It is interesting that only females are known of typical M. concolor, while

mostly males are known of M. nigripennis. Possibly specimens identified here as M. concolor and M. nigripennis are conspecific. Additional adult specimens and detailed rearing of northern Queensland larvae is needed to solve this problem. Locality data for these unassociated larvae from north Queensland are listed here: 12 km N Kuranda, 4.xii.1982, J.T. Doyen, (ANIC, 5); 17.06S 145.34E, 3 km WbyS Mt. Haig, 1150 m, 3.iv.1984, A. Calder & T. Weir, (ANIC, 3); 17.16S 145.47E, Mulgrave R. Rd., 7 km WbyS Bellenden Ker, 2.iv.1984, A. Calder & T. Weir, (ANIC, 9); Mt. Lewis, 20 km S Mossman, 1000 m, 10.vii.1982, S. & J. Peck, (ANIC, 5); 6° 03'S x 145° 25'E, Mt. Halcyon, 850 m, 22-24.xi.1993, G.B. Monteith, (QMBA, 4).

Natural History

No previously published information was available on the natural history or biology of Morpholycus species, except for purported mimetic associations, as discussed below. Label data and my personal observations are the sources of data for this section. I collected larvae of Morpholycus under the bark of dead trees of a variety of taxa: Eucalyptus regnans, E. delegatensis R.T. Baker, E. saligna Sm., E. pilularis Sm., E. microcorys F. Muell., Nothofagus cunninghamii, N. moorei, Acacia dealbata Link. (Leguminosae), and Ceratopetalum apetalum D. Don (Cunoniaceae). Also, larva, pupae and adults were collected from under bark of several unidentified rainforest hardwoods. A single larva of M. monilicornis was collected under bark of Pinus radiata D. Don. (Pinaceae).

Most collections of specimens of Morpholycus are from various types of rainforest, including cool and warm temperate, and subtropical. However, larvae were collected beneath the bark of Eucalyptus in dry and wet sclerophyll forests, also. As well, specimens were collected over an elevational gradient of 300 - 1300 m.

Larvae feed apparently on the decaying cambial-phloem layer present beneath the outer bark, much in the same way as Pytho larvae feed subcortically in dead coniferous trees (Pollock 1991). This material has the consistency of humus, and is reasonably moist; larvae excavate channels as feeding progresses. From the information available, the timing of the life cycle cannot be ascertained. However, I collected prepupae or pupae from late November to mid-January. Larvae construct elliptical pupal cells from the decaying inner bark material, and undergo a prepupal, quiescent stage, before pupation occurs. This pupal stage lasts probably about 10 days, dependent upon local conditions.

In several locations in NE New South Wales, and SE Queensland, larvae of at least two species of Morpholycus were found syntopically, under bark of a single dead tree. On Mt. Glorious, Queensland, larvae of M. monilicornis, M. costipennis, and M. apicalis were collected in very close proximity to one another. Thus, rearing of larvae, as described above, was the only method of obtaining positively associated larvae and adults.

Adults were collected from different types of foliage, and from malaise traps. The lobed tarsal segments, toothed tarsal claws and large eyes are thought to be adaptations for this active habit (Watt 1987). Mating and oviposition were not observed.

Adults of at least one species of Morpholycus have been recognized as being involved in a Batesian - Müllerian mimetic assemblage centred around the genus Metriorrhynchus Guér. (Coleoptera: Lycidae) (Moore and Brown 1989). Other mimics in this group include members of Stigmodera Esch. (Buprestidae), Palaestra Lap. (Meloidae), Pseudolycus Guér. (Oedemeridae), Stenocentrus McK., Eroschema Pasc., Tritocosmia Newm. (Cerambycidae), Rhinotia Kirby (Belidae), and Snellinia lineata (Walk.) (Lepidoptera: Stathmopodidae).

Geographical distribution

Based on the specimens collected to date, the range of the genus Morpholycus extends from southern Victoria to extreme northern Queensland. The distribution follows generally the Great Dividing Range; specimens have not been collected west of this system. Morpholycus is apparently absent from Tasmania.

Relationships (Fig. 270)

The genus Morpholycus is one of the more relatively derived genera of Pilipalpinae, and is the adelphotaxon of Cycloderus. These two genera are in turn collectively the adelphotaxon of Binburrum. Synapomorphies of Cycloderus + Morpholycus are mentioned above, in the treatment of Cycloderus.

Key to Species of Morpholycus Based on Adults

1(0). Antennae in both sexes moniliform to subfiliform (Fig. 13); inner apex of elytra developed as small tooth (various in size, absent in a few specimens); secondary elytral setae all erect, curved (Fig. 125); accessory lobes narrow, sinuate (Figs. 148, 161) ..... M. monilicornis Lea

Antennae serrate or pectinate (Figs. 14-20); inner elytral apex rounded, not developed into tooth; secondary elytral setae either inconspicuous (Fig. 126), or if erect, then not curved (Fig. 127); accessory lobes subquadrate, not sinuate (Figs. 162-165).....2

2(1). Pronotum entirely yellow or red, without contrasting black markings.....3

Pronotum entirely black, or red/yellow with contrasting black markings.....5

3(2). Elytron entirely black, or in some specimens with small red humeral spot; legs entirely dark ..... M. nigripennis (Macleay)

Elytron entirely yellow / red or bicoloured with black (one specimen examined with entirely black elytra with yellow patches on base of femora) 4

4(3). Elytron yellow basally, with ± truncately margined, apical black area, extended to apex of elytron (one specimen examined with elytra uniformly black); scutellum yellow; legs with at least basal part of front femur yellow; male with distinctly pectinate antennae (Fig. 19); females with subpectinate antennomeres (Fig. 20).....M. flabellicornis (Macleay)

Elytron entirely pale, or with obliquely margined, apical black area; scutellum black; legs black; male unknown; female antennomeres serrate ....M. concolor (Macleay)

5(2). Pronotal vestiture reduced, not conspicuous (Figs. 103-104); elytra with distinctly raised carinae (Fig. 126); elytral vestiture not conspicuous (Fig. 126); antennae of male serrate (Fig. 14).....M. costipennis Lea

Pronotal vestiture conspicuous, whorled (Figs. 105-106); elytra with suggestions only, of carinae; elytral vestiture conspicuous (Fig. 127); antennae of male pectinate (Fig. 17). .....M. apicalis (Macleay)

Key to Species of Morpholycus Based on Known Larvae

1(0). Urogomphal pits widely separated by broad, projecting intra-urogomphal process (Fig. 218); basolateral margin of urogomphal plate not produced laterally; urogomphi divergent at their apices; posterolateral angle of T8 produced into blunt dentiform process (Fig. 223)..... M. monilicornis Lea

Urogomphal pits closer together; intra-urogomphal process projecting or not; if so, then very narrow, acutely pointed (Fig. 219); basolateral margins of urogomphal plate produced laterad bases of urogomphi (Figs. 219-220); urogomphi subparallel or convergent apically; posterolateral angle of T8 not produced into blunt dentiform process (e.g. Fig. 224).....2

2(1). Intra-urogomphal process narrow, acute, projecting to near midlength of inner urogomphal tooth (Fig. 219); inner urogomphal teeth stout, positioned near base of urogomphi; urogomphi distinctly convergent apically ....M. costipennis Lea

Intra-urogomphal process not projecting (Fig. 220); inner urogomphal teeth relatively slender, positioned near midlength of urogomphi; urogomphi subparallel, only slightly convergent apically .....M. apicalis (Macleay)

Morpholycus monilicornis Lea

Figs. 13, 101-102, 125, 136, 148, 160-161, 184, 218, 223, 261

Morpholycus monilicornis Lea 1917: 290. TYPE MATERIAL: LECTOTYPE (SAMA) (here designated, indicated by 'TY', on left side of card with two specimens), male; labelled: "monilicornis Lea, Type Bulladelah / I 6655 Morpholycus monilicornis N.S. Wales [this label with 'TYPE' in red ink along right margin]". TYPE LOCALITY: Australia, New South Wales, Bulladelah. PARALECTOTYPES (SAMA), one male, right specimen on same plate as lectotype, same label data; one male, labelled: "Clifton / Co-type / 18978 Morpholycus monilicornis Lea N.S.W: V: [this label with 'Cotype' in red ink along right margin]"; one female (?), labelled: "Dorrigo N.S. Wales / Co-type / Ditto Var. 1 Vic: N.S.W:"; two males mounted on one card, labelled: "3912 / Ditto Var. 1 Vic: N.S.W:".

Specific epithet.—From the Latin nouns monilis, meaning string of beads, and cornus, meaning horn, in reference to the characteristic antennomere shape in this species.

Adult

Diagnosis.—Antennae moniliform to subfiliform in both sexes (Fig. 13); lateral margin of pronotal disc rounded, variously tuberculate or smooth (Fig. 101); lateral edge of elytron posterad midlength concealed dorsally; apex of elytral suture with small tooth; males with accessory lobes elongate, sinuate, acutely pointed distally (Figs. 148, 161).

Description.—TL 7.9 - 13.0 mm; GEW 2.4 - 3.8 mm. Head. Antennae moniliform to subfiliform (Fig. 13); antennomeres slightly more elongate in males. Pronotum (Figs. 101-102). Disc with lateral margins rounded, with or without several tubercles; lateral depressions subcircular, delimited by transverse ridges; setae erect, sparse. Elytra (Fig. 125). Disc with suggestions of 2 longitudinal carinae; lateral edge not visible dorsally posterad midlength; suture developed apically into short tooth; primary setae very short, inconspicuous; secondary setae long, erect, curved apically. Male genitalia (Figs. 148, 161). Accessory lobes elongate, sinuate, acutely pointed apically. Colour. Colour of several forms; head, pronotum, appendages, and venter uniformly dark in both forms; elytra either uniformly rufous except sutural margin and epipleuron anterad midlength; or rufous with variously developed dark vitta, contiguous across suture anteriorly with inner margins divergent posteriorly; some specimens with elytra almost entirely dark; dark vitta with or without violaceous lustre; one specimen with uniformly rufo-testaceous pronotum, dark elytra, and light areas on the profemora; one specimen with head, pronotum and elytra dark, except for the anterior pronotal margin, rufous; one specimen with pronotum and anterior 1/5 of the elytra yellow, rest of body black.

Taxonomic notes.—Three specimens from northern Queensland share most of the diagnostic features of typical M. monilicornis, but differ in several aspects. One male specimen from Lamb Range, Emerald Creek has filiform antennae, entirely rufo-testaceous pronotum, dark elytra and profemora with proximal half rufotestaceous. Pronotal and elytral setation are similar to M. monilicornis. The sutural apices of the elytra are developed as small teeth, but the posterior half of the lateral elytral margin is visible dorsally. The accessory lobes are very similar to M. monilicornis, but not exactly the same shape. The TL of this specimen is 6.5 mm, shorter than any other examined specimen of M. monilicornis.

The second specimen is also a male, and is from Windsor Tableland, 35 km NNW Mt. Carbine. This individual has subfiliform antennae, and the head, pronotum and elytra are dark, except for the anterior pronotal margin, rufous. The elytral sutural tooth is absent

and the lateral elytral margin is visible posteriorly. The setation on the pronotum and elytra are similar to that of M. monilicornis, as are the accessory lobes. Like the above specimen, the shape of the accessory lobes is not exactly the same as in M. monilicornis, and the TL is 6.1 mm.

The third specimen is from near Mt. Spurgeon, NE Queensland, and exhibits distinct variation in colour from typical, more southern M. monilicornis, and also from the two specimens described above. The pronotum and anterior 1/5 of the elytra are yellow, as are bases of the front femora and venter of the head. The rest of the body is black. The antennae are submoniliform, and the elytral setae are identical to those of typical M. monilicornis. This body colour is almost identical to that of typical M. flabellicornis, with which this specimen is sympatric. It is possible that both this form of M. monilicornis and M. flabellicornis are mimicking the same species of Lycidae.

Larva

Diagnosis.—Basolateral margins of urogomphal plate not produced laterally (Fig. 218); urogomphi divergent apically; intra-urogomphal process very wide, subtruncate posteriorly; urogomphal pits widely separated; dorsal surface of urogomphal plate with complete transverse row of tubercles; posterolateral angle of T8 produced as blunt, dentiform process (Fig. 223).

Description.—posterolateral angle of T8 produced as blunt, dentiform process (Fig. 223); basolateral margins of urogomphal plate not produced laterally (Fig. 218); urogomphi with outer margins subparallel, divergent slightly posteriorly, apices divergent posteriorly; inner urogomphal teeth situated approximately half length urogomphi; approximate ratio of maximum width of urogomphal plate : distance between urogomphal apices —1.0; intra-urogomphal process very wide, transverse, projecting posteriorly; posterior margin subtruncate, approximately 4 times wider than long; urogomphal pits small, widely separated; punctulae small; setiferous tubercles 2 per side; additional tubercles forming transverse row across posterior region of urogomphal plate.

Geographical Distribution (Fig. 261)

Morpholycus monilicornis is relatively widespread, and is the only species of Morpholycus known from Victoria. Its range extends along the coast without significant gaps north to near the Brisbane area. A large gap separates the most northerly locality of these records, and the localities (one larval, two adult) from north Queensland.

Material examined. I examined 43 adults and 260 larvae, from the following localities:

ADULTS. **Australian Capital Territory**. Brindabella Range, Blundells Ck. Rd. 1000 m, 3.xii.1988, H. & A. Howden, (CMNC, 1). **New South Wales**. 28.29 S, 152.54 E, Tooloom Plateau 14 km W. Urbenville, 14.ii.1984, I.D. Naumann, (ANIC, 1); 35.35 S 149.55 E, Monga State Forest, 26.xi.1979, G. Medvedev, (ANIC, 2); 48 km. N. Singleton, 13-15.xi.1981, H. & A. Howden, (CMNC, 1); Barrington Tops Nat. Pk., Gloucester R, 32.04 S 151.32 E, on surface at night, 12-14.xi.1981, A. Calder, (ANIC, 1); Blue Mts., no other data, (AM, 1); Bulladelah, no other data, (SAMA, 2); Bulladellah, H. Stephens, ex Ferguson, (BMNH, 1); Dilgry River, Barrington Tops S.F., 31.53 S 151.32 E, 15-16.xi.1981, T. Weir, (ANIC, 1); Dorrigo, no other data, (SAMA, 1); Dorrigo, W. Heron, (AM, 1); Hwy 52, 2.9 km E jct. Hwy 52 & Monga State Forest Road, 700 m, 30.xi.1990, Pollock & Reichert, under bark of Eucalyptus, (DAPC, 1); Lansdowne St. Forest, Peninsula Rd., in dry scler. forest, 3.xi.1981, G. & T. Williams, (ANIC, 1); "Lorien" W.R. 3 km N. Lansdowne Taree; ex. r/f margin; malaise trap, G. Williams, 30.xi-6.xii.1987, (ANIC, 1); 4-11.x.1987, (ANIC, 2); 27.xii.1987-3.i.1988, (ANIC, 1); 18-27.xii.1987, (ANIC, 1); 15-22.xi.1987, (ANIC, 1); 10-17.i.1988, (ANIC, 2); Monga State Forest, Milo Forest Road, ca. 700 m, 30.xi.1990, Pollock & Reichert, under bark of Eucalyptus sp, (DAPC, 2); Moruya R, 15 km NW Moruya, 3.x.1982, J. Doyen, (CASC, 1); Mt. Royal Rng., 36 km E. Moonan Flat, 7.xi.1982, J. Doyen, (ANIC, 1). **Queensland**. NE QLD, Emerald Ck, Lamb Range, 950 m, 11.x.1982, Monteith, Yeates & Thompson, (ANIC, 1); NE Q, 16°22'S x 145°13'E, 7 km N. Mt. Spurgeon (Camp 2), 17-19.x.1991, 1200-1250 m, Monteith, Janetzki, Cook &

Roberts, (QMBA, 1); SE Qld. Mt. Glorious, 13.ii.1961, L. & M. Gressitt, (BPBM, 1); SE Qld. Mt. Glorious, sclerophyll forest, 16-20.ii.1961, L. & M. Gressitt, (BPBM, 1); Tamborine Mtn., Macdonald National Park, 550 m, 12.i.1991, Pollock & Reichert, reared from larva coll. under bark of hardwood, (DAPC, 1); Windsor Tbld., 35 km NNW Mt. Carbine, N. Qld., 1050 m, 15-18.iv.1982, Monteith, Yeates & Cook, (QMBA, 1). **Victoria**. Cumberland Scenic Reserve, nr. Cambarville, 37.43S 145.53E, 7-9.xii.1990, Pollock & Reichert, coll. in pupal cells under bark of Eucalyptus regnans, (DAPC, 9); Warragul, no other data, J.C. Goudie, (SAMA, 1).

LARVAE. **Australian Capital Territory**. Blundells Ck. Rd., 3 km E Piccadilly Circus, 24.x.1982, J.F. Lawrence, (ANIC, 1); Condor Ck., Uriarra Forest, 12.ix.1982, J.T. Doyen, under bark Pinus radiata, (ANIC, 1). **New South Wales**. 28.48S 152.59E, Richmond Range S.F., ca. 600 m, 13-14.ii.1983, T. Weir & A. Calder, coll. under bark, (ANIC, 3); Barrington Tops, Barrington House, 420 m, 16.vi.1978, S. & J. Peck, log & bark litter, (ANIC, 2); Bellangry State Forest, Wilson River Preserve, Palm Glade Walk, 305 m, 22.xii.1990, Pollock & Reichert, under bark of rainforest hardwood, (DAPC, 5); Border Ranges National Park, Antarctic Beech Picnic Area, 1000 m, ca 35 km NW Kyogle, 4.i.1991, Pollock & Reichert, under bark of Noth. moorei, (DAPC, 6); Border Ranges National Park, Bar Mtn. Picnic Area, ca 800 m, 25 km N. Kyogle, 5.i.1991, Pollock & Reichert, under bark of hardwood, (DAPC, 7); Border Ranges National Park, Sheepstation Creek Rest Area, 375 m, 8.i.1991, Pollock & Reichert, under bark Eucalyptus, dry sclerophyll forest, (DAPC, 5); Chichester St. For, Lagoon Pinch Pack, 8.xi.1982, J. Doyen, (ANIC, 1); Chichester State Forest, Allyn River Forest Park, ca 20 km N. Dungog, 490 m, 24.xii.1990, Pollock & Reichert, under bark of Eucalyptus laevipennis, (DAPC, 5); Chichester State Forest, Burraga Swamp Walk, off Mt. Allyn Road, ca 45 km NW Dungog, 920 m, 25.xii.1990, Pollock & Reichert, under bk. Nothofagus moorei in cool temperate rainforest, (DAPC, 15); Chichester State Forest, Telegherry Forest Drive, nr. The Mountaineer Reserve, ca 35 km N. Dungog, 905 m, 19.xii.1990, Pollock & Reichert, under bark of Nothofagus moorei, (DAPC, 8); Gibraltar Ranges National Park, Atrichornis Trail, 900 m, ca 60 km E. Glen Innes, 2.i.1991, Pollock & Reichert, (DAPC, 5); Hwy 52, 2.9 km E jct. Hwy 52 & Monga State Forest Road, 700 m, 30.xi.1990, Pollock & Reichert, under bark of Eucalyptus, (DAPC, 7); Kioloa St. For., 4-5.iii.1986, J. & N. Lawrence, under bark & in rotten logs, rainforest, (ANIC, 10); Macquarie Pass National Park, Picnic Area on Albion park end of Illawarra Hwy, 200 m, 22.i.1991, Pollock & Reichert, under bark in rainforest, (DAPC, 12); Monga, 27.ix.1977, Lawrence & Weir, (ANIC, 13); Moonpar State Forest, N.W. Jolly Memorial Grove, 675 m, ca 15 km N. Dorrigo, 27-28.xii.1990, Pollock & Reichert, under Eucalyptus and hardwood bark, (DAPC, 9); New England N.P., Wrights Lookout, 11.x.1960, E. Britton, (ANIC, 3); New England National Park, Cascade Walk, ca 80 km E. Armidale, 1200 m, 30.xii.1990, Pollock & Reichert, under bark of tallowood and Noth. moorei, cool temperate rainforest, (DAPC, 19); New England National Park, Lyrebird Nature Walk, ca. 80 km E. Armidale, 1300 m, 1.i.1991, Pollock & Reichert, (DAPC, 17); New England National Park; Nightcap National Park, Matheson Trail, ca 35 km N. Lismore, 8.i.1991, Pollock & Reichert, under bark, (DAPC, 6); Nightcap National Park, Pholi's Walk, 35 km N. Lismore, 8.i.1991, Pollock & Reichert, under bark, warm temperate / subtropical rainforest, (DAPC, 1); Styx River State For., nr forestry HQ, 1000 m, ca 70 km E. Armidale, 31.xii.1990, Pollock & Reichert, under Eucalyptus bark in dry sclerophyll forest, (DAPC, 2); Werrikimbe National Park, Cobcroft Rest Area, ca 70 km ESE Walcha, 1100 m, 18.i.1991, Pollock & Reichert, under bark of lge. Eucalyptus sp., (DAPC, 5); Werrikimbe National Park, Plateau Beech Picnic Area, cool temperate rainforest walk, ca 70 km ESE Walcha, 1100 m, 22-23.xii.1990, Pollock & Reichert, under bark of Nothofagus moorei, (DAPC, 22); Whian Whian State Forest, Minyon Falls Picnic Area, 350 m, ca 30 km N. Dorrigo, 29.xii.1990, Pollock & Reichert, (DAPC, 5); Wiangaree S.F., Brindle Ck., 29.ii-3.iii.1980, Newton & Thayer, (ANIC, 2); Wildcattle Creek St. Forest, Wodong Picnic Area Trail, ca 25 km N. Dorrigo, 500 m, 29.xii.1990, Pollock & Reichert, (DAPC, 6); Willow Forest Road, 4.3

km N Nerriga, 575 m, 2.xii.1990, Pollock & Reichert, under bark Eucalyptus in dry sclerophyll forest, (DAPC, 10). **Queensland**. 17.06S 145.34E, 3 km WbyS Mt. Haig, 1150 m, 3.iv.1984, A. Calder & T. Weir, (ANIC, 1); Brisbane Forest Park, Mount Glorious State Forest, nr. Mt. Glorious Village, 14-15.i.1991, Pollock & Reichert, under bark, (DAPC, 5); Bunya Mountains National Park, Paradise Picnic Area, ca 50 km SW Kingaroy, 1000 m, 17.i.1991, Pollock & Reichert, under bark, (DAPC, 6); Bunya Mountains National Park, Westcliff Track, ca 50 km SW Kingaroy, ca. 1000 m, 16.i.1991, Pollock & Reichert, under bark, rainforest, (DAPC, 5); Lamington N.P., Binna Burra, 25.iii-4.iv.1985, J. & N. Lawrence, under bark & in rotten wood, (ANIC, 2); Lamington National Park, Border Trail, nr. O'Reillys, 920-1000 m, 11.i.1991, Pollock & Reichert, under bark, (DAPC, 7); Maiala N.P., Mt. Glorious, 600 m, 4.vii.1978, S. & J. Peck, under bark, (ANIC, 5); Tamborine Mtn., Macdonald National Park, 550 m, 12.i.1991, Pollock & Reichert, under bark, palm rainforest, (DAPC, 10). **Victoria**. Acheron Gap, near Warburton, 750 m, 30.iv.1978, S. & J. Peck, debris under bark of Euc. regnans, (ANIC, 2); Cambarville Rec. Area, Cumberland Scenic Preserve, 37.43S 145.53E, ca. 1000 m, 8.xii.1990, Pollock & Reichert, under bark of Eucalyptus regnans, (DAPC, 10).

Morpholycus costipennis Lea

Figs. 14, 65-67, 103-104, 126, 162, 208-214, 219, 262

Morpholycus costipennis Lea 1917: 290. TYPE MATERIAL: LECTOTYPE (SAMA) (here designated, indicated by 'TY', on right side of card with two specimens), male; labelled: "costipennis Lea Type Tambourine / Morpholycus I.6656 costipennis Queensland [this label with 'TYPE' in red ink along right margin]". PARALECTOTYPES (SAMA), one female, same label data as lectotype; one female, labelled: "Tam Mt. Hacker 1/07 / Co-type / 19227 Morpholycus costipennis Lea Var. Queensland [this label with 'Cotype' in red ink along right margin]". TYPE LOCALITY: Australia, Queensland, Tamborine Mountain.—Lea 1921: 218; Lawrence and Britton 1991: 662 (Fig. 35.52 I), 669 (Fig. 35.56 B).

Specific epithet.—From the Latin nouns costa, meaning rib, and penna, meaning wing, in reference to the distinct longitudinal elytral costae in this species.

Adult

Diagnosis.—Antennae serrate in both sexes (Fig. 14); paired pronotal depressions deep, distinct laterally; elytra each with four distinctly convex, longitudinal carinae traceable to near apex; setae on pronotum and elytra very short, inconspicuous (Figs. 104, 126); males with accessory lobes subtriangular, widened and truncate apically (Fig. 162).

Description.—TL: 8.2 - 12.3 mm; GEW: 2.2 - 4.0 mm. Head. Antennomeres 3-10 serrate in both sexes (Fig. 14); antennomeres in male slightly more produced and elongate. Pronotum (Figs. 103-104). Disc with lateral margins rounded, somewhat angulate at widest point posterad midlength; lateral depressions deep, variously divided into smaller depressions by transverse ridges; setae very short, inconspicuous. Elytra (Fig. 126). Disc with four distinctly developed longitudinal carinae, visible to near apex; lateral margin of visible dorsally posterad midlength; primary setae short, length less than diameter of punctures; secondary setae short, restricted to carinae, not recurved apically. Male genitalia (Fig. 162). Accessory lobes broad, subtriangular, widened and truncate apically. Colour. Dorsum of head black; pronotum orange and black; centre of pronotal disc black, with orange colouration restricted to margins, variously developed; scutellum black; elytral colour of two forms: some specimens with elytra uniformly rufous except for narrow sutural infuscation posterad midlength; other specimens with apical 1/3 of elytra black, anterior margin of black area divergent posteriorly; epipleuron rufous in both colour forms; venter and appendages dark, gula and abdominal ventrites somewhat lighter.

Larva

Diagnosis.—Intra-urogomphal projection acute, produced posteriorly (Fig. 219); inner urogomphal teeth inserted near base of urogomphi; basolateral margins of urogomphal plate produced laterally, truncate.

Description.—Basolateral margins of urogomphal plate produced laterally, truncate (Fig. 219); urogomphi with outer margins convergent posteriorly, apices convergent posteriorly; inner urogomphal teeth situated near base; approximate ratio of maximum width of urogomphal plate : distance between urogomphal apices —3.5; intra-urogomphal process acutely pointed, projecting posteriorly; approximate ratio of intra-urogomphal process width : length —1.5; urogomphal pits large; punctulae large, conspicuous; setigerous tubercles two per side.

Geographical Distribution (Fig. 262)

Morpholycus costipennis has a range extending from north central New South Wales, north to southern Queensland (from 27 - 33° S. latitude). All localities were from the eastern extensions of the Great Dividing Range.

Material examined. I examined 39 adults and 243 larvae from the following localities:

ADULTS. **New South Wales**. 23-31 km NE Wiangaree, 23.xi.1982, J. & E. Doyen, (DAPC, 1), (ANIC, 2); 28.22S 153.05E, Wiangaree St. For., 1050 m, 10-12.ii.1983, T. Weir & A. Calder, "by sweeping", (ANIC, 1); 32.08 S 151.27 E, Allyn River, Chichester S.F., 10-11.xi.1981, T. Weir & A. Calder, (ANIC, 1); Acacia Plat[eau], J. Armstrong, (BMNH, 1); Barrington Tops St. For., Cobark Forest Park Trail, ca. 40 km WNW Gloucester, 1050 m, 23.xii.1990, Pollock & Reichert, on veg. in cool temperate Noth. rainforest, (DAPC, 1); Border Ranges Nat. Pk., Sheepstation Creek campground, Rosewood Loop Trail, 5.i.1991, Pollock & Reichert, reared from larva, (DAPC, 1); Dorrigo National Park, Rosewood Creek Trail, nr. Dorrigo, 700 m, 28.xii.1990, Pollock & Reichert, hand picked off veg., rainforest, (DAPC, 1); Dorrigo, 1.11.1911, (QMBA, 1); Nightcap Nat. Pk., Philo's Walk, 650 m, ca 35 km N. Lismore, 8.i.1991, Pollock & Reichert, reared from prepupa coll. under hardwood bark, (DAPC, 1); Pipeclay Ck. Rd., Lansdowne State Forest, 5.x.1980, in rotting log in rain forest, G. & T. Williams, (ANIC, 1); Richmond River, 1909, (BMNH, 1); Salisbury, 1000 ft., 15.ii.1932, Darlington, (MCZC, 1). **Queensland**. 5 km SE Rathdowney, Qld. NSW, 11.i.1981, J. Powell, (ANIC, 1); 27.56 S 153.11 E, Witches Falls N.P., Tamborine Mt., 21.x.1978, under bark, Lawrence & Weir, (ANIC, 1); 27.56 S 153.12 E, Joalah N.P., Tamborine Mt., 18-21.x.1978, Lawrence & Weir, (ANIC, 2); 27.56 S 153.12 E, Joalah N.P., Tamborine Mt., 18-21.x.1978, on low foliage, Lawrence & Weir, (ANIC, 1); 28.14 S 153.08 E, Lamington N.P. (O'Reillys), 22-27.x.1978, reared from under bark, Lawrence & Weir, (ANIC, 4); Lamington Nat. Pk, O'Reillys, Blue Pool Walk, 500 m, 11.i.1991, Pollock & Reichert, reared from larva, (DAPC, 1); Mt. Glorious nr. Brisbane, 635 m, 11.xii.1988, H. & A. Howden, (CMNC, 1); National Park , H. Hacker, xi.1920, (QMBA, 1); xii.1921, (QMBA, 2); xii.1919, (QMBA, 1); National Park [=Lamington National Park], i.1928, Nicholson, (DAPC, 1), (ANIC, 1); Tamborine Mtn., Joalah National Park, Creek Circuit Trail, 550 m, 10.i.1991, Pollock & Reichert, coll. in pupal cell under bark, (DAPC, 1); same data except reared from immature collected under bark, (DAPC, 7); Tamborine Mtn., Palm Grove National Park, 450 m, 12.i.1991, reared from larva coll. under hardwood bark in palm rainforest, Pollock & Reichert, (DAPC, 4); Tamborine Mtn., Macdonald National Park, 450 m, 10.i.1991, reared from larva coll. under hardwood bark in palm rainforest, Pollock & Reichert, (DAPC, 4); Tambourine, S.E.Q., 8.12.1947, C.L. Sandercock, (QMBA, 1); Tam. Mts., no other data, (BMNH, 1).

LARVAE. **New South Wales**. Bellangry State Forest, Wilson River Preserve, Palm Glade Walk, 305 m, 22.xii.1990, Pollock & Reichert, under bark of rainforest hardwood, (DAPC, 5); Border Ranges National Park, Antarctic Beech Picnic Area, 1000 m, ca 35 km NW Kyogle, 4.i.1991, Pollock & Reichert, under bark Noth. moorei, (DAPC, 1); Border Ranges National Park, Bar Mtn. Picnic Area, ca 800 m, 25 km N. Kyogle, 5.i.1991, Pollock & Reichert, under bark hardwood, (DAPC, 4); Border Ranges National Park, Rosewood Loop Trail, 375-500 m, 5-6.i.1991, Pollock & Reichert, under bark in rainforest, (DAPC, 3);

Border Ranges National Park, Sheepstation Creek, Booyong Trail, 6.i.1991, Pollock & Reichert, (DAPC, 6); Dingo Tops St. Forest, Bulga Forest Drive, Dingo Tops Forest Park, ca 30 km N. Wingham, 925 m, 20.i.1991, Pollock & Reichert, under bark, (DAPC, 20); Gibraltar Ranges National Park, Atrichornis Trail, ca 60 km E. Glen Innes, 900 m, 2.i.1991, Pollock & Reichert, under bark in wm. temp. rainforest, (DAPC, 7); New England Nat. Pk, Wrights Lookout, 11.x.1966, E. Britton, (ANIC, 2); Nightcap National Park, Pholi's Walk, ca 35 km N. Lismore, 8.i.1991, Pollock & Reichert, under bark, warm temperate / subtropical rainforest, (DAPC, 6); Werrikimbe National Park, Cobcroft Rest Area, Carabeen Track, ca 70 km ESE Walcha, 1050 m, 18.i.1991, Pollock & Reichert, under bark, (DAPC, 6); Werrikimbe National Park, Plateau Beech Picnic Area, ca 70 km ESE Walcha, 1100 m, Pollock & Reichert, under bark Nothofagus moorei, (DAPC, 1); Whian Whian State Forest, Minyon Falls Picnic Area, 350 m, ca 30 km NE Lismore, 3.i.1991, Pollock & Reichert, (DAPC, 5); Wiangaree S.F., Brindle Ck, 29.ii-3.iii. 1980, Newton & Thayer, (ANIC, 7). **Queensland**. Brisbane Forest Park, Mount Glorious State Forest, nr. Mt. Glorious Village, 14-15.i.1991, Pollock & Reichert, under bark, (DAPC, 35); Lamington N.P, Nr. O'Reillys, 22-27.x.1978, Lawrence & Weir, (ANIC, 10); 2-4.iii.1980, under bark & in rotten wood, (ANIC, 10); Lamington N.P., x.1978, (DAPC, 3); Lamington Nat. Pk., Binna Burra, 25.iii-4.iv.1985, J. & N. Lawrence, under bark and in rotten wood, (ANIC, 4); Lamington National Park, Border Trail, nr. O'Reillys, 920-1000 m, 11.i.1991, Pollock & Reichert, under bark, (DAPC, 20); Mt. Glorious, Maiala N.P., 600 m, 4.vii.1978, under bark, S. & J. Peck, (ANIC, 9); Tamborine Mtn., Joalah N.P., 18-21.x.1978, Lawrence & Weir, (ANIC, 5 larvae & 2 pupae); 22.vi.1978, S. & J. Peck, (ANIC, 10); Tamborine Mtn., Joalah National Park, Creek Circuit Trail, 550 m, 10.i.1991, Pollock & Reichert, under bark in rainforest, (DAPC, 38); Tamborine Mtn., Macdonald National Park, 550 m, 12.i.1991, Pollock & Reichert, under bark, palm rainforest, (DAPC, 13); Tamborine Mtn., Palm Grove National Park, 450 m, 10.i.1991, under hardwood bark in palm rainforest, Pollock & Reichert, (DAPC, 13).

Morpholycus apicalis (Macleay)

Figs. 17-18, 105-106, 127, 164, 220, 224, 226, 264

Pseudolycus apicalis Macleay 1872: 313. TYPE MATERIAL: LECTOTYPE (AMSA), male; labelled: "[orange-red disc] / 700 / K 35381 / Pseudolychus apicalis [some illegible writing] Gayndah / HOLOTYPE / Austr. Mus. Collection". PARALECTOTYPE (AMSA), male; labelled: "[orange disc] / K35381 / ♂ / HOLOTYPE / Austr. Mus. Collection". TYPE LOCALITY: Australia, Queensland, Gayndah.—Blackburn 1899: 72, 84.—Blair 1914: 311.—Schenkling 1915: 22.—Lea 1917: 288.—Arnett 1950: 222.

Notes on type specimens.—Both type specimens of Pseudolychus apicalis bear holotype labels. Therefore, the more complete of the two specimens was designated as lectotype, with the other being the single paralectotype. Both individuals exhibit the apicalis colour form.

Specific epithet.—A Latin adjective derived from the noun apex, meaning top, referring to the apical dark elytral markings seen in the types of this species.

Adult

Diagnosis.—Antennomeres pectinate in males (Fig. 17), serrate-subpectinate in females (Fig. 18); head black dorsally; pronotal disc orange and black, in some specimens almost entirely black; elytra a combination of orange and black, with suggestions of 3 longitudinal carinae; male with accessory lobes rectangular, long margins subparallel, distal margin emarginate (Fig. 164).

Description.—TL 8.0 - 11.8 mm; GEW 2.4 - 3.7 mm. Head. Antennomeres 3-10 serrate-subpectinate in females (Fig. 18); pectinate in males (Fig. 17). Pronotum (Fig. 105-106). disc with lateral margins subparallel or slightly convergent anteriorly; lateral depressions shallow, subdivided between anterior and posterior margins; setae long, conspicuous, somewhat whorled laterad central concavity; mostly decumbent on disc,

erect along margins. Elytra (Fig. 127). Disc with no, or faint suggestions of longitudinal carinae; lateral margin visible posterad midlength; primary setae at least twice as long as diameter of punctures; secondary setae conspicuous, uniformly distributed, not recurved apically. Male genitalia (Fig. 164). Male accessory lobes subrectangular, long margins subparallel, emarginate distally. Colour. Dorsum of head dark; pronotal and elytral colour of two forms: some specimens with pronotum rufotestaceous except for central longitudinal black vitta, widened posteriorly, subtended by lateral depressions; these specimens with elytra rufotestaceous, each elytron with variously developed, longitudinal, posteriorly divergent, dark region, not extended to elytral apex; other specimens with lighter colour of pronotum restricted to extreme lateral margins; these specimens with elytra rufotestaceous with posterior 1/4 to 1/3 black, extended to epipleuron; venter and appendages uniformly dark in both forms.

Larva

Diagnosis.—Outer basal margins of the urogomphi subparallel (Fig. 220); intra-urogomphal process not protruding posteriorly; inner urogomphal tooth inserted near midlength of urogomphus.

Description.—Basolateral margins of urogomphal plate produced laterally, lobate (Fig. 220); urogomphi with outer margins subparallel, apices distinctly bent inward; inner urogomphal tooth situated near midlength of urogomphus; ratio of maximum width of urogomphal plate : distance between urogomphal apices approximately 2; intra-urogomphal process transverse, subtruncate, not produced conspicuously posteriorly; approximate ratio of lip width: length —3.75; urogomphal pits small; setiferous tubercles two per side; punctulae small in diameter.

Taxonomic notes.—Reared larvae of M. apicalis are quite similar to four larvae collected in association with adults of M. nigripennis and M. concolor. This is discussed above under the taxonomic notes for larval Morpholycus.

Geographical distribution (Fig. 264)

Morpholycus apicalis is known from north central New South Wales to Queensland. The northern extent of its range is approximately 25° S.

Material examined. In addition to the types, I examined 99 adult and 80 larval specimens, from the following localities:

ADULTS. **New South Wales**. "Lorien" W.R., 3 km N Lansdowne / Taree, 3-10.i.1988, G. Williams, ex r/f margin malaise trap, (ANIC, 1); 6-13.xii.1987, G. Williams, (ANIC, 1); Chichester St. For., Allyn River Park, 32°08'S 151°27'E, 410 m, 18-25.xii.1990, Pollock & Reichert, malaise trap in r/f., (DAPC, 1); Dorrigo National Park, Rosewood Trail, nr. Dorrigo, 700 m, 28.xii.1990, Pollock & Reichert, hand picked off veg., (DAPC, 1); Mt. Warning, Up. Tweed R., 11.1.1923, A. Musgrave, (AM, 1); N. Dorrigo, 4.1.1923, A. Musgrave, (AM, 1); The Dorrigo, 3000 ft., W. Heron, (ANIC, 1); The Island Bellinger, Bellinger R., 8.iii.1981, B.J. Day, (AM, 1); Tweed River, no other data, (SAMA, 1). **Queensland**. Austral forest via Bulburin, site 3, 24°34'S 151°29'E, malaise trap, 20.iii.1975, D.K. McAlpine (AM, 2); same data, 22.iii.1975, (AM, 1); same data, 23.iii.1975, (AM, 1); Blackall Range, Coll. Hacker, (BMNH, 1); Brisbane Forest Park, Mt. Glorious St. For., nr. Mt. Glorious village, ca 500 m, 14-15.i.1991, Pollock & Reichert, coll. as adult under bark, (DAPC, 1); reared from prepupae and pupae, (DAPC, 3); Brookfield, 16.iii.1927, H. Hacker, (QMBA, 1); Bulburin, site 1, Monto Distr., 24°31;S 151°29'E, Alt. 540 m, ex. malaise trap, 20.iii.1975, D.K. McAlpine, (AM, 1); Lamington National Park, Blue Pool Walk, from O'Reillys, 500 m, 11.i.1991, Pollock & Reichert, reared from immature collected under bark, (DAPC, 6); Maleny, no other data, H. Hacker, (QMBA, 1); Monto District, Bulburin (Austral), site 3, 24°34'S 151°29'E, Alt. 580 m, 19.iii.1975, D.K. McAlpine, (AM, 1); Mt. Tambourine, 7.11.11, (QMBA, 1); Mt. Tambourine, no other data, (SAMA, 2); Mt. Tambourine, x.1924, A. Musgrave & C. Geissmann, (AM, 1); Nat. Pk. [=Lamington Nat. Pk.], 3000 ft., iii.1929, A.J. Turner, (QMBA, 1); National Park [=Lamington National Park], xii.1921, H. Hacker, (QMBA, 3); xii.1919, H. Hacker, (QMBA,

2); Samford, 19.iii.1922, H. Hacker, (QMBA, 1); Tamborine Mtn., Joalah National Park, Creek Circuit Trail, 550 m, 10.i.1991, Pollock & Reichert, reared from immatures collected under bark, (DAPC, 49); same data, except collected as adults under bark (in pupal cells), (DAPC, 5); Tamborine Mtn., Palm Grove National Park, 450 m, 10.i.1991, Pollock & Reichert, coll. in pupal cell under bark, (DAPC, 3); Tambourine Mt., 1.12, HJC, (SAMA, 1); Tomewin Range, Upper Currumbin, 17.x.1988, G.B. Monteith, (QMBA, 1).
LARVAE. **New South Wales**. New England National Park, Wrights Lookout, 11.x.1966, E. Britton, (ANIC, 1); Richmond Range State Forest, 28.48S 152.59E, ca. 600 m, 13-14.ii.1983, T. Weir & A. Calder, (ANIC, 6). **Queensland**. Brisbane Forest Park, Mount Glorious State Forest, nr. Mt. Glorious Village, 14-15.i.1991, Pollock & Reichert, under bark, (DAPC, 6); Lamington National Park, Binna Burra, 25.iii-4.iv.1985, J. & N. Lawrence, under bark & in rotten wood, (ANIC, 12); Lamington National Park, Blue Pool Walk, from O'Reillys, 500 m, 11.i.1991, Pollock & Reichert, under bark, (DAPC, 10); Tamborine Mtn., Joalah National Park, Creek Circuit Trail, 550 m, 10.i.1991, Pollock & Reichert, under bark in rainforest, (DAPC, 42); Tamborine Mtn., Palm Grove National Park, 450 m, 10.i.1991, under hardwood bark in palm rainforest, Pollock & Reichert, (DAPC, 3).

Morpholycus concolor (Macleay)
Figs. 15, 265

Palaestrida concolor Macleay 1887: 323. TYPE MATERIAL: HOLOTYPE (ANIC), sex unknown; labelled: "Cairns / on permanent loan from MACLEAY MUSEUM University of Sydney; HOLOTYPE / Palaestrida concolor, Macl. Russel R. N. Queens". TYPE LOCALITY: Australia, Queensland, Russel River.—Borchmann 1917: 166.—Lawrence 1987: 361.

Specific epithet.—From the Latin adjective concolor, meaning of the same colour, in reference to the uniform yellow colour of the holotype of this species.

Adult

Diagnosis.—Antennae serrate in females (Fig. 15), condition in males unknown; head dark, with lighter basal area; pronotal disc uniformly orange; mesoscutellum black; elytral disc uniformly orange, or in some specimens, with apical black portion.

Description.—TL: 9.6 - 12.2 mm; GEW: 2.6 - 4.0 mm. Head. Antennae serrate in females (Fig. 15). Pronotum. Disc with lateral margins subparallel, rounded anteriorly and posteriorly, widest posterad midlength; lateral pronotal depressions shallow, uninterrupted from anterior to posterior margins; setae long, somewhat whorled laterad central concavity; mostly decumbent on disc, erect along lateral margins. Elytra. Disc with suggestions of 3 longitudinal carinae; lateral margin visible dorsally posterad midlength; primary setae mostly decumbent, approximately twice as long as diameter of punctures; secondary setae decumbent with few scattered erect setae. Colour. Dorsum of head dark from antennal insertion to behind eyes; labrum and clypeus testaceous; posterior part of head, pronotum, and elytra rufotestaceous dorsally, in most specimens examined; scutellum black; one specimen with anterior third only of the elytra rufotestaceous, separated from dark apical 2/3 by jagged line; all appendages and venter dark, except for head between gular sutures and prosternum.

Geographical distribution (Fig. 265)

Morpholycus concolor is known only from northern Queensland; all of the few specimens examined were collected near Mareeba.

Material Examined. In addition to the type, I examined eight specimens from the following localities:

ADULTS. **QUEENSLAND**. Davis [=Davies] Creek N.P., 10 km E Mareeba, 17-24.ii.1984, L. Masner, malaise trap in rain & sclerophyll forest, (ANIC, 1); Mt. Lewis, 960 m, 16.35S 145.17 E, collected in rainforest, 30.x.1976, R.W. Taylor & T.A. Weir, (ANIC, 1); NE QLD, 22 km S.E. of Mareeba, 900 m, 4.xi.1983, D.K. Yeates & G.I. Thompson, (QMBA, 1); NE QLD. Bell Peak North 10km E Gordonvale, 900-1000m, pyrethrum knockdown, RF,

13.x.1982, Monteith, Yeates & Thompson, (QMBA, 1); nr. Plane Crash, 11 km NW Mossman, 27.ix.1989, 1240 m, ANZSES Expedition, (QMBA, 1); 6° 03'S x 145° 25'E, Mt. Halcyon, 850 m, 22-24.xi.1993, G.B. Monteith, (QMBA, 3) these last two not found / mapped.

Morpholycus flabellicornis (Macleay)

Figs. 19-20, 165, 200, 266

Palaestrida flabellicornis Macleay 1887: 324. TYPE MATERIAL: LECTOTYPE (ANIC) (here designated), male; labelled: "Cairns / On permanent loan from MACLEAY MUSEUM University of Sydney / Syntype / [header label provided with specimens: Palaestrida flabellicornis Macl. Russell R. N. Queens]". PARALECTOTYPE (ANIC), male, same label data as lectotype, head and pronotum missing. TYPE LOCALITY: Australia, Queensland, Russel River.—Borchmann 1917: 166.—Lawrence 1987: 361.

Specific epithet.—From the Latin nouns flabellum, meaning fan, and cornus, meaning horn, in reference to the antennomere shape in males of this species.

Diagnosis.—Antennae markedly pectinate in males (Fig. 19), serrate-subpectinate in females (Fig. 20); head black dorsally except light basal region behind eyes; pronotal disc uniformly orange; greater than posterior half of elytra black, delimited from orange anterior portion by jagged, oblique line; elytra with suggestions of 3 longitudinal carinae; male with accessory lobes rectangular, long margins subparallel, distal margin truncate (Fig. 165).

Description.—TL: 7.9 - 8.9 mm; GEW: 2.4 - 2.5 mm. Head. Antennae serrate-subpectinate in females (Fig. 20), distinctly pectinate in males (Fig. 21). Pronotum. Disc with lateral margins subparallel; lateral depressions shallow, uninterrupted from anterior to posterior margins; setae long, conspicuous, decumbent and somewhat whorled laterad central concavity; few erect setae along lateral margins. Elytra. Disc with suggestions of 3 longitudinal carinae; lateral edge visible posterad midlength; primary setae decumbent; secondary setae erect, not distinctly recurved apically. Male genitalia (Fig. 165). Accessory lobes subrectangular, long margins subparallel; distal margin straight. Colour. Dorsum of head dark anteriorly to level of eyes; clypeus dark except for anterior margin; labrum testaceous; posterior part of head, pronotum, and basal 1/4 to 1/5 of elytra rufotestaceous; posterior portion of elytra dark; elytra uniformly dark in one specimen examined; scutellum testaceous; appendages dark, except bases of femora in most specimens.

Geographical distribution (Fig. 266)

Morpholycus flabellicornis has been collected in north and north central Queensland, between 17 and 20° S. latitude. Most of the specimens examined are from the Cairns region.

Material examined. In addition to the types, I examined 12 specimens from the following localities:

ADULTS. **Queensland**. L. Barrine, Atherton Tab., 2300 ft. 15.iv.1932, Darlington, (ANIC, 1); Cleveland Bay, no other data, (ANIC, 2); 8 km W Kuranda, 20.xii.1986, H. & A. Howden, malaise trap, (ANIC, 1); 17.03S 144.37 E, 2 km NbyE Mt. Tiptree, 800 m, 1.iv.1984, A. Calder & T. Weir, on fallen logs at night, (ANIC, 1); N. QLD, Millaa Millaa Falls, 4.i-7.iii.1990, Storey and Halfpapp, malaise trap, (QPIM, 1); Kuranda, 18.ii.1909, E. Bryant, (BMNH, 1); same, except Feb. 1909, (BMNH, 1); Wongabel S.F., 6 km S. of Atherton, malaise trap, 10.ii-13.iii.1984, Storey and Brown, (QPIM, 1); ditto, MDPI intercept trap, site no. 18, 9.i-10.ii.1984, Storey and Brown, (QPIM, 1); Windsor T'land [=Tableland], 25.ii.1992, R.I. Storey, at UV light, (QPIM, 1); Mt. Bartie Frere, N. Qld., West Slopes, 800-1000 m, 30.xii.1989, G.B. Monteith, (QMBA, 1).

Morpholycus nigripennis (Macleay)

Figs. 16, 163, 263

Palaestrida nigripennis Macleay 1887: 324. TYPE MATERIAL: LECTOTYPE (ANIC), left specimen on card with two specimens, sex unknown; labelled: "Cairns / On permanent loan from MACLEAY MUSEUM, University of Sydney / SYNTYPE / Palaestrida nigripennis Macl. Mossman River N. Queens". TYPE LOCALITY: Australia, Queensland, Mossman River.—Borchmann 1917: 166.—Lawrence 1987: 361.

Morpholycus serraticornis Lea 1917: 289. TYPE MATERIAL: LECTOTYPE (SAMA) (here designated from two syntypes, indicated by 'TY'), male, labelled: "serraticornis Lea Type Cairns / I.6654 Morpholycus serraticornis Lea Queensland [this label with 'TYPE' in red ink along right margin]". PARALECTOTYPE (SAMA), male, with same label data as lectotype. TYPE LOCALITY: Australia, Queensland, Cairns District.—Lawrence 1987: 361.

Notes on type specimens.—Of the two type specimens of Palaestrida nigripennis, glued to the same cardboard plate, the left one agrees with Macleay's description, but the right specimen is Morpholycus flabellicornis. Since Macleay did not indicate a holotype, the single specimen agreeing with his description is designated as a lectotype.

Specific epithet.—From the Latin adjective niger, meaning black, and noun penna, meaning wing, pertaining to the dark elytral colour of this species.

Diagnosis.—Antennae serrate in both sexes (Fig. 16); head mostly dark, with light region basally in most specimens; pronotal disc uniformly reddish or piceous; elytra uniformly piceous to black, or with small humeral orange spot in some specimens; longitudinal elytral carinae only very faintly suggested or absent; males with accessory lobes subrectangular, long margins divergent distally; upper (away from median lobe) apical angle enlarged, lobate (Fig. 163).

Description.—TL: 7.8 - 8.7 mm; GEW: 2.2 - 2.5 mm. Head. Antennae (Fig. 16) serrate in males and females, antennomeres only slightly less produced in females. Pronotum. Disc with lateral margins subparallel, very indistinctly rounded; lateral depressions shallow, elongate, uninterrupted from anterior to posterior margins; setae dense, decumbent and erect; decumbent setae somewhat whorled laterad central concavity. Elytra. Disc with no, or only faint suggestions of longitudinal carinae; lateral margin posterad midlength visible dorsally; length of primary setae greater than diameter of punctures; secondary setae short, not recurved distally. Male genitalia (Fig. 163). Accessory lobes subrectangular, long margins divergent distally, upper apical angle enlarged, somewhat lobe. Colour. Head dark from antennal insertion to behind eyes; labrum and clypeus testaceous; posterior part of head and pronotum rufous; scutellum and elytra dark, some specimens with small rufous humeral spot; venter and appendages uniformly dark; one specimen examined with entire dorsal surface uniformly piceous.

Geographical distribution (Fig. 263)

Morpholycus nigripennis has been collected only in the region near Cairns, northern Queensland.

Material examined. In addition to the types, I examined eight specimens from the following localities:

ADULTS. **Queensland**. 12 km N Kuranda, 4.xii.1982, J.T. Doyen, (ANIC, 1); Endeavour River, no other data, (ANIC, 1); Danbulla S.F., 13 km NE of Yungaburra, 26.iii-23.iv.1987, Storey and De Favari, malaise trap, (QPIM, 2); Mt. Lewis Road, NE Qld, 11 km from Highway, 18.xii.1989 - 13.i.1990, site 1, 1000m, Flt. intercept, Monteith, Thompson, ANZSES, (QMBA, 1); 16° 03'S x 145° 25'E, Mt. Halcyon, 850 m, 22-24.xi.1993, G.B. Monteith, (QMBA, 3) these last 2 records not found / mapped.

Placement of Palaeopyrochroa crowsoni Abdullah

The Tertiary fossil record available for the salpingid group families is very sparse. Lithomacratria mirabilis Wickham from the Florissant Shales (late Eocene or early Oligocene), is placed in Pedilinae (Pyrochroidae) (Young 1984). Abdullah (1965) described the genus Palaeopyrochroa from Baltic amber and placed it in Pyrochroidae, allied to forms with appendiculate tarsal claws, i.e. Pilipalpinae. According to Abdullah (1965) the visible characters on the fossil preclude its placement in any tenebrionoid family other than Pyrochroidae. These characters (taken from Abdullah 1965) are: 1) tarsi 5-5-4; 2) tarsi with lobed penultimate tarsomere; 3) abdomen with all ventrites freely articulated; 4) front coxae projecting; 5) front coxal cavities open behind; 6) prothorax without side borders; 7) mesepimera reaching middle coxal cavities; 8) front coxal cavities open, trochantins exposed; tarsal claws appendiculate, tibial spurs simple.

An examination of the holotype of Palaeopyrochroa crowsoni (UHGI) revealed characters that may place the specimen among the Pilipalpinae, and others which possibly unite it with Pyrochroinae or Pedilinae (sensu Young 1984). Family placement of the specimen cannot be ascertained positively. Characters shared by Palaeopyrochroa and (Pyrochroinae + Pedilus) are as follows: 1) eyes emarginate near antennal base, and 2) pronotum with very wide, trough-like posterior bead. The specimen has visibly appendiculate tarsal claws, somewhat intermediate to the states seen in Pyrochroinae (absent or only suggested) and Pedilus (distinctly toothed). All species of Pilipalpinae have variously appendiculate tarsal claws, but this feature alone is not sufficient for grouping Palaeopyrochroa with Pilipalpinae. Also, all known species of Pilipalpinae have both the penultimate and antepenultimate tarsomeres at least enlarged, while in Palaeopyrochroa, only the penultimate tarsomere is enlarged and produced ventrad the base of the distal tarsomere. This feature was mentioned by Abdullah (1965), who stated that Palaeopyrochroa was unlike Techmessa, Techmessodes and Exocalopus in not having the antepenultimate tarsomere lobed, and on the differences of head and pronotal shape.

One very obvious character of Palaeopyrochroa is the dimorphic elytral setae, consisting of shorter, decumbent setae and fewer, longer erect setae. This feature is similar to the primary and secondary elytral setae in all genera of Pilipalpinae, but occurs also in Pedilus and other taxa of Tenebrionoidea, in a variety of families.

The pronotum in Palaeopyrochroa is smooth, evenly convex, and without depressions. In this character, Palaeopyrochroa resembles quite closely Dendroides and Pedilus, and has a similar deep groove along the posterior margin of the pronotum.

One feature shared by Palaeopyrochroa and Pedilus is the relatively complete elytral epipleuron. In all genera examined of Pyrochroinae, the epipleuron is traceable only to near the metasternum, while in Pedilus, it is visible, although quite narrow, to at least the third abdominal sternum. This latter condition occurs also in Palaeopyrochroa. Length of the epipleuron is various among genera of Pilipalpinae.

The antennomeres in Palaeopyrochroa are serrate, and are similar to antennomeres of female pyrochroines like Schizotus and females of Exocalopus. The male of Palaeopyrochroa probably had pectinate or flabellate antennomeres, based on comparison with extant, sexually dimorphic pyrochroines. Discovery of a male specimen of P. crowsoni, although doubtful, would be particularly illuminating, especially if the genitalia are extruded as they are in the female holotype.

In summary, various characters tie Palaeopyrochroa to Pilipalpinae, and still other characters ally this genus with Pedilus or Pyrochroinae. The specimen could also be a representative of some other tenebrionoid family such as Melandryidae. Abdullah (1965) placed great importance on the appendiculate tarsal claws, placing Palaeopyrochroa among Pilipalpinae. The lack of expansion of the antepenultimate tarsomere in

Palaeopyrochroa would seem to be a better character, for placing the genus possibly in Pyrochroinae, and not in Pilipalpinae. Unfortunately, the one known specimen of Palaeopyrochroa is a female, otherwise the decisive characters of the male tegmen might have been visible in the specimen. Palaeopyrochroa crowsoni could be a pyrochroid, but this is not certain. Because of this uncertainty, this fossil species was excluded from further phylogenetic analysis.

Evolutionary considerations

Reconstructed phylogeny of genera of Pilipalpinae

Introduction

As mentioned above, Watt (1987) provided the first hypotheses of relationship among the family-group taxa Trictenotomidae, Salpingidae, Boridae, Pythinae, and Pilipalpinae, and I used these as a starting point for my own analysis of the relationships among taxa of the salpingid group. Pilipalpinae were demonstrated to be monophyletic (Pollock 1994), and the primary goal of the present work is to postulate the phylogenetic relationships among genera of Pilipalpinae.

A major impediment to this goal was the apparent paucity of unique and unreversed phylogenetic characters among the genera of Pilipalpinae. Synapomorphies are few, whereas autapomorphies are relatively common. A major reason for this could be that the genera have been separated geographically for an exceedingly long time and have diverged distinctly with respect to external structure, of both adults and larvae.

Analysis of Characters

In the discussion of characters below, states are given for genera of Pilipalpinae, Tydessinae, Pyrochroinae and Pedilinae, and for Boridae. For all characters, a zero indicates the hypothesized plesiomorphic state; other numerals indicate the hypothesized apomorphic state(s). Although PAUP determines the relative polarity of all characters with respect to maximum parsimony (according to specified outgroup), I have provided polarities for all characters. All characters are unordered, i.e. a change of one state to any other state is allowed and is considered to be one step. Brief statements are given below also for the evolution of each character, and whether there is homoplasy and / or reversals in the group examined.

Some of the characters discussed below were used by Pollock (1994) in an analysis of the entire salpingid group; these are repeated in this section (characters 2, 4-5, 7-9, 15-17, 19). For some of these repeated characters, the plesiomorphic character states (coded as 0), are restricted to the outgroup (Pythidae, Boridae, etc.) and are not represented in the ingroup (Pyrochroidae). A summary of the character states are given in Table 4.

Character 1. Antennal sensorium (larva). Two states: 0—raised, conical; 1—low, dome-like. Basis for designation: outgroup analysis. The shape of the sensorium on the apex of antennomere 2 is characteristic of genera in the salpingid group. In most genera of Pilipalpinae, and in Pedilinae and Pyrochroinae, the sensorium is conical, with a distinctly acutely pointed apex. In Boros and Lecontia (Boridae), and in Morpholycus, Cycloderus, Binburrum, and Temnopalpus, the sensorium is flattened and somewhat elliptical. This condition is thought to be apomorphic, and has arisen twice independently in Pilipalpinae: once in the clade consisting of Morpholycus, Cycloderus and Binburrum, and also in Temnopalpus.

Character 2. Urogomphal pits (larva). Three states: 0—one urogomphal pit; 1—two urogomphal pits; 2—no urogomphal pits. Basis for designation: outgroup analysis. Larvae of genera of Pilipalpinae have a pair of urogomphal pits (e.g. Figs. 225-226), with the exception of a single larva of Binburrum which does not possess these pits (see

taxonomic notes for larvae of Binburrum, above). Since only a single larva of Binburrum was found with this condition, its significance is not determinable. A pair of urogomphal pits are present also in larvae of Boridae, Pyrochroinae and Pedilinae. Larvae of the genus Tydessa do not have urogomphal pits (Nikitsky 1986). The single urogomphal pit of Pythinae is postulated as primitive (as indicated by Pollock, 1994), with the double pit the derived, and the total absence of the pit in larvae of Tydessinae the most highly derived state.

Character 3. Number of stemmata (larva). Five states: 0—five stemmata; 1—four stemmata; 2—three stemmata; 3—two stemmata; 4—no stemmata. Basis for designation: generalized outgroup analysis. All examined genera of Pythidae and the genus Boros possess five stemmata per side of the head capsule. Four stemmata are known in larvae of Pedilus and Pyrochroinae. Three stemmata are present in the larva of Tydessa (Nikitsky 1986). Two stemmata per side are present in all genera of Pilipalpinae. Finally, there are no stemmata in Techmessa and Lecontia. A survey of number of stemmata in larval Tenebrionoidea in Lawrence (1991) indicates that five may be the primitive state in the superfamily. Various taxa within, or closely related to, the salpingid group (e.g. Mycteridae, Othniinae, Inopeplinae) in addition to Salpingidae, have five stemmata per side in the larval stage. The condition in Pythidae (five per side) is therefore postulated here the plesiomorphic state, with a loss of stemmata, resulting in the state in Tydessa (three stemmata). The conditions seen in Lecontia and Techmessa represent independent losses from five and two stemmata, respectively. The character in Tydessa provides additional evidence as to the isolation of this genus from genera of Pilipalpinae. Two stemmata per side is a synapomorphy uniting the genera of Pilipalpinae.

Character 4. Shape of maxillary palpomere 4 (adult). Two states: 0—securiform; 1—cultriform. Basis for designation: outgroup comparison. The apical maxillary palpomeres of adults of Trictenotomidae, Salpingidae, Pythidae, Boridae, and Tydessa are variously securiform, while that in Pilipalpinae, Pyrochroinae, and Pedilinae are variously cultriform. This is a postulated synapomorphy for the clade (Pilipalpinae + (Pyrochroinae + Pedilinae)).

Character 5. Pronotal lateral margin (adult). Three states: 0—completely margined; 1—partially margined; 2—unmargined. Basis for designation: outgroup and generalized outgroup comparison. The primitive state of this character is found in Trictenotomidae, Sphalma (Pythidae), and in Boridae. An intermediate state (here the primitive state), in which the lateral margin of the pronotum is margined about half its length, is found in Tydessa (Tydessinae). The most derived condition, that of an entirely smooth lateral margin, is found independently in Salpingidae, Pythidae (all genera except Sphalma), and in (Pilipalpinae + (Pyrochroinae + Pedilinae)). As stated by Lawrence and Pollock (1994) the lateral pronotal carina among genera of Boridae is unique in that it is very fine and deflected ventrally on the pronotum.

Character 6. Elytral epipleuron (adult).—Three states: 0—epipleuron short, visible to only V2 or V3 (Figs. 133-134); 1—epipleuron present to near elytral apex (Fig. 135); 2—epipleuron traceable to, and around elytral apex to sutural margin (Fig. 136). Basis for designation: outgroup analysis. The elytral epipleuron is variously developed throughout the salpingid group. Within Pilipalpinae, the presence of a complete, apically dorsal, elytral epipleuron defines the clade including Morpholycus, Cycloderus, Binburrum, Exocalopus, Techmessa, Techmessodes, Ranomafana and Incollogenius. Within this clade, specimens of Incollogenius, Ranomafana, and some specimens of Binburrum exhibit the intermediate state. Within Binburrum and Incollogenius, both the complete and nearly complete epipleuron is present.

Character 7. Accessory lobes (adult). Two states: 0—present; 1—absent. Basis for designation: outgroup analysis. Watt (1987) used the shared presence of male accessory lobes as a synapomorphy for the salpingid group of families. As mentioned above, the presence of accessory lobes is a primitive, groundplan feature of the salpingid group. The accessory lobes have been lost from all Pyrochroinae (Figs. 173-176) and Pedilinae, and from the genus Sphalma Horn (Pythidae), thus representing two independent derivations of the apomorphic state. Accessory lobes are present in all known genera of Pilipalpinae (Figs. 137-148).

Character 8. Tarsal claw tooth (adult). Two states: 0—absent; 1—present. Basis for designation: outgroup comparison. Tarsal claws of Trictenotomidae, Salpingidae, Pythidae and Boridae are simple, without teeth. Variously developed teeth are present on the tarsal claws of Tydessa, Pilipalpinae, and Pedilinae, but not in Pyrochroinae. I postulate that the state in Pyrochroinae represents a reversal from the derived state.

Character 9. Tarsomere shape (adult). Two states: 0—penultimate tarsomere lobed; 1—antepenultimate and penultimate tarsomeres lobed. Basis for designation: outgroup comparison. There are a variety of tarsomere shapes among taxa of the salpingid group, correlated with habits of the adults of these taxa. Adults of Trictenotomidae, Salpingidae, Pythidae and Boridae are relatively non-vagile and have primitive non-lobed tarsomeres. Adults of Tydessa, Pilipalpinae, Pyrochroinae, and Pedilinae are more active on vegetation or flowers, and have variously lobed tarsomeres. Adults of Pyrochroinae have only the penultimate tarsomere lobed, while the other above mentioned taxa have at least the antepenultimate and penultimate tarsomeres lobed ventrally.

Character 10. Elytral setae (adult). Three states: 0—not dimorphic, inconspicuous; 1—not dimorphic, conspicuous; 2—dimorphic. Basis for designation: outgroup analysis. Adults of Boridae have inconspicuous, decumbent setae, restricted to elytral punctures (Fig. 107). Adults of Pyrochroinae have longer, erect setae, restricted also to the elytral punctures (Fig. 111). In adults of Pilipalpinae, two types of elytral setae are present. Most setae on a single elytron are decumbent, and are inserted just slightly anterad the elytral punctures; these are termed the primary elytral setae. Scattered among these punctures and decumbent setae are larger erect, and/or curved setae (termed secondary elytral setae). All genera of Pilipalpinae (Figs. 112-127) as well as Pedilus (Fig. 110), have this dimorphic type of elytral setae. The one adult of Tydessa blaisdelli examined has the primary setae inserted within the elytral punctures (Fig. 108), while all other taxa examined, had the setae inserted outside of, and just anterad, the elytral punctures. Very short primary elytral setae are present in T. blaisdelli as well as in Paromarteon (Fig. 112). Short primary elytral setae are also present in some species of Morpholycus and most species of Cycloderus (Figs. 120-127). This latter occurrence may be a reversal to the plesiomorphic state and / or be significant in the mimetic relationships in these two genera.

Character 11. Elytral punctation (adult). Three states: 0—punctures small; 1—punctures of moderate size; 2—punctures large, faveolate. Basis for designation: outgroup analysis. Elytral punctures of Boridae are small and shallow (Fig. 107). Punctures of Tydessinae (Figs. 108-109) Pyrochroinae and Pedilus are very small and are only slightly greater in diameter than the seta (Figs. 110-111). Within Pilipalpinae, several types of elytral punctures are present. In Paromarteon (Fig. 112), Temnopalpus (Figs. 113-114), and Pilipalpus (Fig. 115), the punctures are elliptical, and are only slightly greater in diameter than the decumbent elytral setae. This may be the condition in Malagaethes also, although SEM analysis was not done to confirm this. In Paromarteon and Tydessa blaisdelli, the decumbent elytral setae are inserted within the punctures. In

the remaining genera of Pilipalpinae, the punctures are larger, reaching a maximum in species of Cycloderus (Figs. 120-124) and Morpholycus (Figs. 125-127).

Character 12. Insertion of accessory lobes (adult). Two states: 0—lobes inserted basad midlength of apicale; 1—lobes inserted toward apex of apicale. Basis for designation: outgroup analysis. Watt (1987) postulated that long, slender accessory lobes arising more proximally on the apicale represented the plesiomorphic condition. Shorter accessory lobes arising more distally on the apicale were hypothesized by Watt to represent the apomorphic condition. A comparison with other taxa of the salpingid group bears this out. However, Watt used this character state as a synapomorphy for the entire Pilipalpinae, although he had not examined all genera. In fact, Tydessa (Pollock 1994b) and Paromarteon (Fig. 137) exhibit Watt's primitive condition. The remaining genera possess shorter accessory lobes which are inserted toward the apex of the apicale. Certain species of Binburrum exhibit the primitive state (e.g. Fig. 143), but this is likely a reversal from the apomorphic state.

Character 13. Punctation of pronotum (adult). Three states: 0—punctures small, inconspicuous; 1—punctures umbilicate; 2—punctures deep, faveolate. Basis for designation: outgroup analysis. Most members of the salpingid group have small, simple pronotal punctures, not significantly greater in diameter than that of the setae arising from them. Within Pilipalpinae, three types of pronotal punctures are represented. The primitive state is that which most closely resembles the condition in Boridae and Pyrochroinae. This small, non-umbilicate pronotal puncture is found in Paromarteon (Figs. 83-84) and in Tydessa blaisdelli (Tydessinae). The intermediate state is the umbilicate, non-faveolate punctures. These punctures are considerably larger in diameter than their setae, and have a built up area immediately around the base of the setae (Figs. 88, 90, 92). This type of puncture is found in all remaining genera, except for Cycloderus and Morpholycus. Pilipalpus has a double row of large umbilicate punctures along the midline of the pronotum, with the remaining pronotal punctures of the primitive, smaller, non-umbilicate form. Temnopalpus and Malagaethes have comparatively small umbilicate punctures separated by greater than the average diameter of the punctures. Umbilicate pronotal punctures of Binburrum, Techmessodes, Techmessa, Exocalopus, Incollogenius, and Ranomafana are larger and more closely spaced. One species of Binburrum, B. concavifrons, has punctures resembling neither the umbilicate nor faveolate states (Fig. 85-86). All species of Morpholycus (Figs. 101-106) and most species of Cycloderus (Figs. 93-100) have the faveolate type pronotal puncture. These punctures are quite deep and approximate to each other, separated by distinct walls or ridges. Two species of Cycloderus, C. hirsutus (Figs. 93-94) and C. immaculicollis have pronotal punctures intermediate between the umbilicate and faveolate type. This is postulated to represent a reversal.

Character 14. Shape of posterior pronotal margin (adult). Three states: 0—margin truncate; 1—margin medially emarginate; 2—margin distinctly trisinuate. Basis for designation: outgroup analysis. Most taxa of Tenebrionoidea, including the majority of the salpingid group, have a straight or only slightly, medially sinuate posterior pronotal margin. The pronotal margin in Boridae, Pyrochroinae and Pedilus is only slightly emarginate medially. Within Pilipalpinae, the pronotal margin is truncate in Paromarteon, Temnopalpus, Malagaethes, Ranomafana, and Pilipalpus. The margin is slightly emarginate medially in Techmessa and Incollogenius, and distinctly trisinuate in Techmessodes, Exocalopus, Binburrum (Fig. 85), Cycloderus (Figs. 93, 95, 97, 99), and Morpholycus (Figs. 101, 103, 105).

Character 15. Punctulae on abdominal tergites (larva). Two states: 0—absent; 1—present. Basis for designation: outgroup analysis. In larvae of Pilipalpinae, punctulae are found not only on the urogomphal plate, but also on several abdominal tergites. Extensive areas of punctulae are absent from abdominal tergites of larvae of all other salpingid group taxa. This larval feature is postulated tentatively as a synapomorphy for genera of Pilipalpinae, pending discovery of larvae of the pilipalpine genera Pilipalpus, Malagaethes, Ranomafana, and Incollogenius.

Character 16. Bursal glands (adult). Two states: 0—present; 1—absent. Basis for designation: in and outgroup comparison. This character is included in the analysis despite the fact that homologies and identity of the structures in the female reproductive tract in Tenebrionoidea are not clear. Any structure which is attached to the distal end of the bursa is thought to be a gland. Such structures are found in Trictenotoma sp., some pythines, in all salpingids examined, in Boridae (Fig. 185, g), and in Tydessa (Fig. 186, g), although the dissections of the latter were difficult to interpret due to inadequate preparations. Possession of these 'glands' is postulated to represent the primitive state, with their loss as the derived state. Females of Pilipalpinae (Figs. 177-184), Pyrochroinae (Fig. 187), and Pedilinae (Fig. 188) are without these possibly glandular structures.

Character 17. Three-branched spermatheca (adult). Two states: 0—absent; 1—present. Basis for designation: outgroup comparison. Slender, three-branched spermathecae were found in all examined genera of Pilipalpinae (Figs. 177-184), and not in females of any other taxa of the salpingid complex. The lack of these structures in females of Tydessa (Fig. 186) was one of the reasons why this genus was separated from Pilipalpinae. This structure is one of the most convincing synapomorphies for the genera in Pilipalpinae. It is not known whether these branches represent three separate spermathecae, or whether they represent a single, three-branched spermatheca.

Character 18. Mandibular mola (adults). Two states: 0—large, subquadrate; 1—narrow; 2—absent. Basis for designation: outgroup / ingroup analysis. Within the salpingid group, several general conditions are seen for shape and extent of the mandibular mola. A relatively large mola is present in Tydessa (Fig. 69) and Paromarteon (Fig. 39), as well as in Boros (Fig. 30). The actual structure of the mola differs among taxa. In Sphalma (Fig. 25), and Boros, the mola is emarginate anteriorly, surrounding the prostheca. The sculpturing on the mola is clearly transverse, and consists of small, rectangular teeth. In the remainder of Pilipalpinae (except Techmessa) and in Pyrochroinae and Pedilus, the mola is relatively narrow, widest anteriorly. The mola in Cyclodenus (Fig. 63) is relatively wider than other Pilipalpinae. A unique condition characterizes Techmessa, where the mola is absent, or at least indistinctly sclerotized and thickened (Fig. 54). For most taxa, feeding behaviour is unknown, but the absence of a mola in Techmessa and certain Salpingidae may indicate predatory food habits, and this would be considered a derived feeding habit within the salpingid group.

Character 19. Posterior pronotal pits (adult). Two states: 0—absent; 1—present. Basis for designation: outgroup comparison. A pair of small, deep pits near the posterolateral angles of the pronotum is an autapomorphy for the genus Tydessa. This feature is one of several unique characters of larvae and adults of this genus, and is illustrated in Pollock (1992b), Figs. 4-5.

Character 20. Parabasal ridges (larva). Two states: 0—present; 1—absent. Basis for designation: outgroup analysis. All larvae of the salpingid group except Priognathus (Pythidae) and Temnopalpus have sclerotized ridges along the anterior

margins of the abdominal tergites and meso- and metathoracic tergite (e.g. Figs. 204, 207). The presence of these ridges is considered a primitive character state for the entire salpingid group, while their absence is an autapomorphy for Temnopalpus.

Character 21. Inner urogomphal teeth (larva). Two states: 0—present; 1—absent. Basis for designation: outgroup analysis. This larval feature is of great potential importance in the phylogeny of the salpingid group. However, its presence or absence is difficult to interpret. Inner urogomphal teeth characteristic of larvae of Pythidae, most Pilipalpinae, some Salpingidae, Pedilus, and one genus of Pyrochroinae (Pogonocerus thoracicus Fisch.) (Kelejnikova and Mamaev 1981). Urogomphal teeth are absent from Boridae, Tydessa (Tydessinae), and Exocalopus (Fig. 233). Within Pilipalpinae, the loss of the teeth is considered to be an autapomorphic character loss, for larvae of Exocalopus. This may also have occurred in Pyrochroinae, in which Pogonocerus has the primitive character state.

Character 22. Antennomere shape (adult). Four states: 0—moniliform; 1—filiform; 2—serrate / pectinate. Basis for designation: outgroup and generalized outgroup analysis. Although this character is excellent for species and genus-level taxonomy, its value in phylogenetic analysis is difficult to assess. Antennomere shape is various and diverse through the salpingid group. Adults of Pythidae and Salpingidae have short filiform antennae with a very slightly developed, apical club. Adults of Boridae have moniliform antennomeres. Adults of Pyrochroinae have sexually dimorphic antennae, in which females have serrate or slightly pectinate antennomeres, and males with distinctly pectinate antennomeres. Antennomeres of Pedilus spp. are either serrated-flabellate and are also sexually dimorphic in some species. The male of Anisotria shooki Young (Pedilinae) has the basal eight antennomeres moniliform to slightly filiform, with antennomeres 9-11 elongate filiform (Young 1984).

Within Pilipalpinae, moniliform, or short filiform antennomeres are present in Paromarteon (Fig. 1), Temnopalpus (Fig. 2), Malagaethes (Fig. 3) Ranomafana (Fig. 4), and some species of Incollogenius. Elongate filiform antennae occur in Pilipalpus (Fig. 6), Techmessa (Fig. 8) Techmessodes (Fig. 9), Binburrum (Fig. 7), and Cycloderus (Fig. 12). Females of Exocalopus have elongate, serrated antennomeres (Fig. 11) while males have elongate pectinate antennomeres (Fig. 10). Finally, in Morpholycus, one species has moniliform to short filiform antennomeres (Fig. 13). Two others display a serrated / pectinate female / male sexual dimorphism (Figs. 17, 18 and 19, 20), with the remainder of species of Morpholycus with serrated antennomeres in both sexes (Figs. 14-16).

Character 23. Asperities on S9 (larva). Three states: 0—present, complete row; 1—single asperity per side; 2—absent. Basis for designation: outgroup analysis. Most members of the salpingid group have larvae with a transverse row of small dentiform asperities along the anterior margin of the abdominal S9. Larvae of Pyrochroinae have a complete transverse, U-shaped, row of asperities, while those of Pedilus are either reduced to a single stout asperity per side (Wharton 1979) or a complete, transverse row (in P. flabellatus [Young and Pollock 1991]). All known larvae of Pythidae have a complete, slightly arcuate row of asperities, as do most genera of Pilipalpinae. The structure of the asperities is most similar between Pyrochroinae and Pilipalpinae, when compared with Pythidae. A unique condition exists in larvae of Techmessa, where the asperities are absent and are marked by small punctures along the anterior margin of S9. This represents an autapomorphy for the genus, or at least for the one species examined.

The discovery of the complete, transverse row of asperities in the larva of Pedilus flabellatus was used by Young and Pollock (1991) as evidence for the hypothesized relationship in Pyrochroidae of Pyrochroinae + Pedilinae + Cononotinae. By outgroup comparison, the single asperity at the anterolateral corners of S9 would represent the

derived state, and the complete transverse row the primitive state. The larva of P. flabellatus is very similar structurally to those of some genera of Pilipalpinae, notably Techmessa, Techmessodes and Cycloderus.

Character 24. Eye margin (adult). Two states: 0—emarginate; 1—margin entire. Basis for designation: outgroup analysis. Almost all taxa in the salpingid group have a complete ocular margin, without emargination. A variously emarginate ocular margin occurs in adults of Boros, Lecontia, Sphalma (all from canthus), Techmessodes, Pyrochroinae and Pedilinae (except Anisotria), and in Palaeopyrochroa crowsoni. If Pyrochroinae and Pedilinae form the best outgroup for Pilipalpinae, then the emarginate ocular margin in Techmessodes represents the primitive character state and the entire ocular margin the derived state.

Character 25. Pronotal depressions (adult). Two states: 0—absent; 1—present. Basis for designation: outgroup analysis. Paired, pronotal depressions characterize some members of Pythidae (Pytho) and Pilipalpinae, and are absent from members of Trictenotomidae, Boridae, Salpingidae, Tydessinae, Pyrochroinae, and Pedilinae. Within Pilipalpinae, these depressions are indistinct in Paromarteon, Temnopalpus, Malagaethes, Incollogenius, Ranomafana, and Techmessa. Depressions are developed variously in the remaining genera of Pilipalpinae, and this is thought to represent a synapomorphy for the genera Techmessodes, Binburrum, Exocalopus, Cycloderus and Morpholycus.

Character 26. Shape of male apicale (adult). Two states: 0—entire or cleft slightly; 1—cleft deeply. Basis for designation: outgroup analysis. Throughout the salpingid group, the male apicale is markedly varied in shape. In most taxa, the apicale is entire, and not deeply cleft and divided into two lobes. However, in males of Paromarteon (Fig. 137) and some species of Binburrum (e.g. Fig. 143), the apicale is deeply cleft. This represents two independent derivations of the apomorphic state of this character.

Character 27. Hypostomal rods (larva). Two states: 0—absent; 1—present. Basis for designation: outgroup analysis. Hypostomal rods are absent from the most examined larvae of the salpingid group. Distinct hypostomal rods are present in larvae of Pyrochroinae, and larvae of Cycloderus and Morpholycus. Individual larvae of Morpholycus vary with respect to presence and relatively length of the hypostomal rods. Therefore, this character is tentatively proposed as a synapomorphy for Cycloderus + Morpholycus, and independently derived in larvae of Pyrochroinae.

Character 28. Bursal spines (adult). Two states: 0—spines absent; 1—spines present. Basis for designation: outgroup analysis. The cuticle of the bursa copulatrix of most examined taxa of the salpingid group is smooth, without ornamentation. Females of Boros (Boridae), Paromarteon, Techmessodes and Cycloderus (Fig. 183) have surface ornamentation on the bursa. In Techmessodes and Cycloderus, this consists of small and large spinules, respectively, which form a ring around the bursa. In Paromarteon (Fig. 177), the spinules are not arranged annularly. Within Pilipalpinae, the three occurrences of bursal spines have been developed independently.

Character 29. Eye shape (adults). Two states: 0—symmetrically convex; 1—asymmetrically convex. Basis for designation: outgroup analysis. In all taxa of the salpingid group, except Temnopalpus and Malagaethes, the eye is symmetrically convex, i.e. the anterior convexity of the eye is equal to the posterior. In the two above mentioned genera, the anterior convexity of the eye is distinctly less than that of the posterior aspect.

This presence of this feature may represent a synapomorphy for these two genera, in addition to the following character.

Character 30. Supra-antennal crest (adults). Two states: 0—absent; 1—present. Basis for designation: outgroup analysis. All genera of Pilipalpinae, except Temnopalpus and Malagaethes have the antennal insertions fully exposed dorsally. In the above two genera, a slight ridge is extended along the lateral margin of the frons, concealing slightly the antennal insertions.

Results

The character matrix used in phylogenetic analysis of Pilipalpinae is given in Table 4. For the analysis, Tydessinae, Pedilinae, and Pyrochroinae were selected as the outgroup taxa. ACCTRAN optimization was used, and all characters were treated as unordered (Fitch parsimony) and of equal relative weights. Due to the relatively large number of taxa, a branch-and-bound search was performed, which produced an estimate of the most parsimonious trees. The 'furthest' addition sequence was used, and the COLLAPSE option was in effect, which produced polytomies. The analysis produced two equally parsimonious trees, each of 57 steps. The only difference between these two trees was that in tree one, Pilipalpus was placed in an unresolved trichotomy with (Temnopalpus + Malagaethes) and the large Ranomafana - Morpholycus clade. In tree two, Pilipalpus was the adelphotaxon to (Temnopalpus + Malagaethes). Tree number one has an identical topology to that of a strict consensus tree derived from these two trees. Tree one had a consistency index of 0.789, and a homoplasy index of 0.351, producing a rescaled consistency index of 0.604.

Evolution of structural features

Homoplasy and reversals.—Based on the reconstructed phylogeny, of 43 apomorphic character states distributed among genera of Pilipalpinae, and subfamilies Tydessinae, Pedilinae, and Pyrochroinae, 33 states (77 per cent) arose once, seven (16 per cent) arose twice, and four (nine per cent) arose three times. The character states arising three times are: 1) larval antennal sensorium low, dome-like; 21) inner urogomphal teeth absent; 22.2) antennomeres serrated / pectinate; and 28) presence of bursal spines. Reversals occurred in six character states: 8) tarsal claw tooth absent (in Pyrochroinae); 9) only penultimate tarsomere lobed (in Pyrochroinae); 10.1) elytral setae non-dimorphic (in Pyrochroinae); 12.1) accessory lobes inserted towards base of apicale (twice, in Paromarteon and some species of Binburrum); 24) eye emarginate (twice, in Techmessodes, and in Pedilinae + Pyrochroinae); and 25) absence of pronotal depressions (in some species of Binburrum).

Mimicry in Pilipalpinae.—Moore and Brown (1989) discussed the Australian lycid Metriorrhynchus Guérin is the purported model for a broad mimetic complex, composed of members of Buprestidae, Pyrochroidae (Morpholycus), Meloidae, Oedemeridae, Cerambycidae, and Belidae. The above taxa have various structural and chemical features which are very similar to their lycid model. For example, adults of most species of Morpholycus have a colour combination of orange and black, serrated or pectinated antennomeres, and variously carinate elytra. Mimicry is possibly widespread in Pilipalpinae, and has accounted, at least partly, for the diversity of structural features seen in the group. A similarly broad spectrum of mimicry may be present in Cycloderus, most species of which have a bi-coloured (orange and black) pronotum and dark elytra. Lawrence (pers. comm.) lists the following as having very similar colouration: several species of Cantharidae, Pyractomena spp. (Lampyridae), Campyloxenus pyrothorax Fairm. (Elateridae), Eucaliga sanguinicollis Fairm. and Germ., Mecopselaphus maculicollis Solier and Platylytra vitticollis Fairm. and Germ. (Oedemeridae). The cantharids or lampyrid are probably the model, with

the other taxa being associated mimics. Below, I will discuss various structural features of adults of Pilipalpinae, and attempt to correlate these with mimetic habits. Not all of these features were treated phylogenetically, however. Most of the evidence presented is based on the genus Morpholycus, with which I am most familiar, and applied speculatively to other pilipalpines.

Colour pattern.—Moore and Brown (1989) stated that in members of Pseudolycus Guérin (Oedemeridae), various colour forms of a single species mimic various sympatric species of Lycidae across an extensive geographical range. Among genera and species of Pilipalpinae, colour polymorphism is widespread. Certain species of Paromarteon, Pilipalpus, Techmessodes, Binburrum, Cycloderus, and Morpholycus exhibit multiple colour forms. At least one colour form in these genera could be considered aposematic, i.e. a combination of orange and black.

Antennomere shape.—Among genera of Pilipalpinae, shape of antennomeres varies markedly. This diversity of form can be at least partly accounted for by mimicry. For example, adults of Temnopalpus are thought to be mimetic with adults of Heteromastix (Cantharidae) (Lawrence and Britton 1991), and species of these two genera have short, moniliform to subfiliform antennomeres. Similarly, adults of Morpholycus are purported to be mimetic with adults of the lycid Metriorrhynchus, both genera of which have species with serrated antennomeres. Morpholycus monilicornis could be mimicing a lycid which has similarly moniliform antennomeres. The very elongate, filiform antennomeres in species of Cycloderus are possibly a component of their mimetic relationships with sympatric species of Cantharidae. The evolutionary significance of antennomere shape in the other genera is unknown.

Body sculpture and punctation.—Ornamentation of the pronotum (Figs. 83-106) and elytra (Figs. 107-127) are both remarkable and varied among genera of Pilipalpinae. Some genera, e.g. Paromarteon (Figs. 83-84, 108) have relatively simple pronotal and elytral punctation. This is in marked contrast to Morpholycus, species of which have deep, faveolate punctation (Figs. 101-106, 125-127). Adults of Metriorrhynchus (Lycidae) have relatively coarse punctation on both the pronotum and elytra, which are mimiced in similar structures in Morpholycus. In addition, the pronotum of Metriorrhynchus and most other Lycidae has carinae separating the pronotal depressions into a number of separate, smaller cells. This feature also is exhibited by adults of species of Morpholycus (Figs. 101, 103, 105). The deep punctation in species of Cycloderus serves possibly a similar purpose. Adults of Morpholycus have at least the suggestions of longitudinal, elytral carinae. Their mimetic model has these carinae also.

Trends in structure of male genitalia.—Males of species of each genus of Pilipalpinae exhibit genitalia distinctive in form and relative proportions of the basale and apicale, shape of, and area of attachment of accessory lobes, and shape of median lobe. As indicated by Figs. 137-148, the shape of the tegmen is varied appreciably among genera; I was unable to discern transformation series for many of the features. Only three male genitalic characters were used in the phylogenetic analysis, one of which (character 7) is an autapomorphy for Pedilinae + Pyrochroinae. Character 12, area of insertion of accessory lobes and 26, shape of apicale, were found to be both homoplastic and reversed in certain genera. Shape of median lobe (Figs. 149-160) is almost as varied as that of the tegmen; no major trends were noticed. Evolution of male genitalia may be more important at the species level, rather than the genus.

Summary of character evolution.—A single apomorphic character state was recognized for 18 of 30 characters, two apomorphic states were recognized for eleven characters, and four apomorphic states were recognized in a single character (number of larval stemmata). For each of the 30 characters, a number of assumptions were possible concerning transformations among individual character states for each (Maddison and Maddison

1992). Because so few distinct transformation series were found in the phylogenetic analysis of genera of Pilipalpinae, I treated all 30 characters as unordered, i.e. a change from a state to any other state is counted as one step (termed Fitch parsimony). For example, change from the plesiomorphic state (0) to either of the apomorphic states 1 or 2 (or 3, 4) is counted as a single step.

Many of the character states were found to be homoplastic and / or reversed, especially when Pedilinae + Pyrochroinae were included in the analysis. As mentioned above, it was difficult to find significant, unreversed synapomorphies among genera of Pilipalpinae. The possible widespread mimicry among genera of Pilipalpinae, and the relatively long duration of separation of the allopatric genera, may have obscured relationships among them.

Geographical history of Pyrochroidae and genera of Pilipalpinae

Introduction

The present distribution of Pyrochroidae is complex, and is a combination of amphitropical and austral disjunct elements. In this section, I deal initially with the distribution of Pyrochroidae and the differing views on the historical origin of amphitropical distributions. Secondly, I will discuss the distribution of genera of Pilipalpinae. For this part, comparisons will be made between the reconstructed phylogeny of pilipalpine genera, and that of the hypothetical breakup of the Gondwanian land mass. A relatively new technique, parsimony analysis of historical biogeography, is discussed and used for Pilipalpinae as well as for comparison of other groups of southern temperate plants and animals.

Distribution of family Pyrochroidae

The distribution of the family Pyrochroidae, as it is currently defined to include Tydessinae, Pilipalpinae, Pedilinae, and Pyrochroinae, exhibits an amphipolar (Crowson 1980), amphitropical (Darlington 1965) or antitropical (Cox 1990) pattern. I prefer the term amphitropical, meaning "on both sides of the tropics." The only described Neotropical pyrochroid, the Brazilian genus Pogonoceromorphus, is not a pyrochroid (Lawrence 1982; Young pers. comm.). The two described species of Pogonoceromorphus belong to Lagriinae (Tenebrionidae) and Eurygeniinae (Anthicidae). One genus of Pyrochroine, Pseudopyrochroa Pic, is found in tropical Asia. It is unknown however whether or not this is a secondary invasion of the tropical zone.

The subfamily Pyrochroinae comprises ten genera in the temperate regions of the Northern Hemisphere (Blair 1928; Young pers. comm.) except for many species of Pseudopyrochroa, as mentioned above. Pedilinae, as reconstituted by Young (1984) includes Pedilus Fischer von Waldheim with about 40 species in the Holarctic region (Pic 1911; Fall 1915; Abdullah 1964c). Also, the monobasic Anisotria Young and the late Eocene or early Oligocene Lithomacratria mirabilis Wickham are in Pedilinae; both are from central North America. The subfamilies Tydessinae, Pedilinae, and Pyrochroinae are mostly north temperate in distribution, and are disjunct from all genera of Pilipalpinae, which are south temperate in distribution. Several other groups of Coleoptera exhibit amphitropical distribution patterns (as summarized by Crowson 1980), including broscine Carabidae, Derodontidae, Peltidae (Trogossitidae), Cryptophagidae, Pythidae, and Nemonychidae.

There are two general explanations for such disjunct amphitropical distributions: dispersal and vicariance. Crowson (1980: 290) offered two hypotheses: 1) the groups concerned formerly had tropical representatives which have become extinct; or 2) that the groups concerned have always been climatically limited, and their crossing of the tropical belt took place during periods of cooler climates in the past. Darlington (1965) stated that

climate is the most important factor in producing amphitropical distributions in animals and plants. Darlington (1965) believed that various amphitropical tribes of Carabidae originated in the northern hemisphere and dispersed southward into South America and Australia, via different dispersal corridors. His two major assumptions in formulating his views on amphitropicality are (from Humphries and Parenti 1986: 84): 1), southern continents were relatively stable during the period of evolution of taxa on the land masses; and 2), taxa occupying these land masses are too young to have been affected by any land movement. These two assumptions are no longer regarded favourably (Humphries and Parenti 1986). They were, however, formulated before convincing evidence of continental drift.

Breakup of Gondwanaland and Vicariance in Pilipalpinae

Geologists have postulated that there existed a southern hemisphere supercontinent, Gondwanaland, divided into West Gondwanaland (Africa and South America) and East Gondwanaland (Madagascar, India, Australia, New Zealand, and Antarctica) (Powell et al. 1981; Cranston and Naumann 1991) during at least some of the Mesozoic Era. According to Smith et al. (1981: 61) there is no accurate way of determining how long Pangaea (northern Laurasia plus southern Gondwanaland) existed before it began breaking apart in the Jurassic .

Although the relative dates of separation of the various components of Gondwanaland vary among authors, there seems to be agreement on the actual order of split [the general summary of the procession of splitting is taken from Cranston and Naumann (1991), Crook (1981), Powell et al. (1981), Rabinowitz et al. (1983), Rosen (1978), and Smith et al. 1981)]. In the Upper Jurassic, an oceanic trench formed between western and eastern Gondwanaland, and a seaway began to open between Australia and Antarctica. The land mass of proto-India was the first major fragment to split off Gondwanaland. This occurred between 130-120 mya (Early Cretaceous), with India moving from about 35° S to 25° S. Madagascar separated from Africa as late as 85 mya (Early Cretaceous) according to Cranston and Naumann (1991), while Rabinowitz et al. (1983) speculate that movement of Madagascar relative to Africa ceased about 120 mya. New Zealand was the next major fragment to leave the Gondwanian complex, and was separated from Antarctica-Australia between 80 and 60 mya by water of oceanic depth. Crook (1981) stated that New Caledonia separated about the same time as New Zealand, and a land bridge may have linked the two land masses during this time. The remainder of Gondwanaland (Antarctica, Australia, and South America) retained its integrity for some time after the separation of New Zealand. South America separated from western Antarctica and Australia separated from eastern Antarctica about 50-60 mya. This simplified account of the breakup of Gondwanaland is depicted in Fig. 273, with the relative dates of separation of the various components. The actual dates of separation are relatively unimportant; the order of separation of the components of Gondwanaland has far greater implications with respect to evolution and speciation within Pilipalpinae and other southern hemisphere groups.

It is tempting to incorporate geological or geographical information into the reconstructed phylogeny of genera of Pilipalpinae a priori. However, the phylogeny of Pilipalpinae presented above was reconstructed without reference to present or historical distributions, and the processes that led to recent configurations of the southern continental land masses. As stated by Mackerras (1970: 190), "...the solutions arrived at can satisfy only in so far as the statements of the zoologists are not coloured by palaeogeographical preconceptions and the findings of the earth scientists are based primarily on non-biological evidence." It is clear that both bodies of evidence are integral, and combine to portray the biogeographical history of any group. However, they should be separately derived, and compared a posteriori.

I suggest that the ancestral pilipalpine(s) were Gondwanian in origin, and their evolution proceeded as the individual land masses moved to their present locations. However, the reconstructed phylogeny of genera of Pilipalpinae does not match exactly this procession of fragmentation of Gondwanaland, indicating possible extinctions or dispersal. Although this vicariance was the underlying factor in the evolution of Pilipalpinae, it is obvious that dispersal (over land) must have been important, also. The ancestral stock of Pilipalpinae was probably widely distributed among the areas to become the present southern continental land masses. Lineages f to o (from Fig. 271) must have differentiated, and have been subject to extinction and relict survival, before the split of Madagascar, Australia, New Zealand and South America isolated these areas from one another. This hypothesis requires an ancient origin for the group, i.e. pre-Tertiary. The genus Incollogenius was isolated from lineages r-w when Madagascar separated from Gondwanaland. The remaining genera were present on, and dispersed among, New Zealand, South America and Australia. At this time, the three presently isolated continental masses were linked by Antarctica, which served as a dispersal corridor. The unresolved relationships among lineages q-r can be accounted for by the separation of New Zealand from Australia, and South America, with Techmessa surviving as a relict in New Zealand. Finally, the split between Australia and South America separated Binburrum (relict in Australia) and Cyclodenus and Morpholycus. Vicariance through continental plate displacement likely was the most important factor in the present distribution of the components of Pilipalpinae. Primitive cosmopolitanism was also a pre-requisite, and required a certain amount of dispersal across Gondwanaland. There is no way of proving, however, that jump dispersal between, for example, Australia and southern South America, occurred over wide oceanic barriers. There may have been, and may still be, dispersal from mainland Australia to Tasmania, or between North and South Island, New Zealand, but this occurred after the main differentiation of the major lineages of Pilipalpinae. It is impossible without evidence, i.e. fossils, to prove that dispersal did or did not occur, but for the postulated vicariant events, there is geological evidence to support my assumption that biotas had at least the opportunity for speciation as a result of these events.

The above scenario calls for an ancient origin to Pilipalpinae, with most of the major radiations occurring in concert with the fragmentation of Gondwanaland. To compare the biogeographical events in Pilipalpinae with those postulated to have occurred in other groups, I selected several papers which had both phylogenetic and biogeographic analyses. The authors of these studies invoked both dispersal and / or vicariance events. For example, pseudopsine Staphylinidae are distributed presently among Holarctica, New World tropics, Chile, and New Zealand. Herman (1975: 256) stated that a western United States origin of the group is possible, with emigration to South America and New Zealand. No actual mechanism was hypothesized for this dispersal, however; vicariance was not discussed.

Shpeley (1986) and Straneo and Ball (1989) invoke combinations of vicariance and dispersal events, in their analyses of the biogeography of Metallicina and Peleciini (Carabidae), respectively. The ancestral stocks of the various extant genera of Metallicina differentiated as Gondwanaland fragmented, with dispersal of vagile populations across open oceanic barriers (Shpeley 1986). Similarly, Straneo and Ball (1989) state that the two major lineages of Peleciini diverged when Australia and Antarctica separated from the remaining Gondwanaland. They invoke a dispersal event from Africa to India, over a possibly short oceanic barrier, as well as dispersal from Middle to South America.

Other forms of trans-oceanic dispersal were discussed and discounted by Thayer (1985) in reference to historical biogeography of Metacorneolabium (Staphylinidae), the present distribution of which encompasses New Zealand, southern South America, and Australia. Thayer disregarded the Holarctic-centered, Old World tropics-centered, and circum-Antarctic dispersal hypotheses, and preferred an explanation involving vicariant events associated with the breakup of Gondwanaland. The ancestral stock of

Metacorneolabium therefore must have a minimum age of between 80-140 my, with most of the major differentiation occurring before the Tertiary. Thayer (1985) stated that the sympatry seen among many extant species is the result of dispersal, but after the vicariant event that isolated them.

It is clear from an examination of these few papers that various combinations of dispersal and vicariance events can be used for explaining austral disjunctions, and virtually any other pattern of distribution. In common to most studies of groups present in the southern continents is the hypothesis of a Gondwanian origin, thus requiring an ancient minimum age for these groups. The original, trans-Antarctic biota was undoubtedly diverse, and was dispersed widely on Gondwanaland. There may have been some differentiation and speciation on pre-drift Gondwanaland, but the major events occurred as its component parts broke away and moved to their present relative positions. It is possible that some trans-oceanic dispersal occurred after this rifting began, but I consider this relatively unimportant in the evolution of Pilipalpinae. The vicariant events associated with fragmentation of Gondwanaland isolated ancestral stocks on Madagascar, New Zealand, Australia, and southern South America. As these stocks differentiated, some lineages went extinct, while others persisted as relicts.

Although no extant Pilipalpinae are known from South Africa or India, it is likely considering the postulated origin and differentiation, that Pilipalpinae historically inhabited these regions, as well as Antarctica. Analyses of fossils found in these regions would corroborate or refute the general hypotheses of phylogeny and biogeography presented here.

Brooks Parsimony Analysis in biogeography

It is relatively easy to postulate a certain chain of events, whether dispersal- or vicariance-type, to explain the present geographical distribution of any monophyletic group. However, it is more important to be able to compare the hypothetical biogeographic events among a number of groups exhibiting similar distribution patterns. There are a number of techniques available for analyzing and comparing historical biogeographical patterns and relationships, all of which treat areas (of endemism) as taxa in a phylogenetic context (Wiley 1988b). There are five general types (Wiley 1988b: 273): 1) reduced area cladogram method; 2) component analysis; 3) Brooks parsimony analysis (BPA); 4) ancestral maps method; and 5) group compatibility methods. The two methods which are most commonly used and / or cited in biogeographic literature are component analysis and BPA. I used BPA to examined the area relationships exhibited by a variety of other taxa.

Brooks (1981) developed the basic tenets of BPA to analyze the coevolution between groups of parasites and their host animals, and to expand upon the parasitological method of absolute ranking of Hennig (1966). The various aspects of BPA have been outlined by
Brooks 1981, 1985, 1990; Brooks and McLennan 1991; Cracraft 1988; Kluge 1988; Wiley 1988a, 1988b; Wiley et al. 1991. The last word on BPA is that of Brooks (1990), and the procedures described therein are those used in my own analyses. The protocol for using BPA outlined below is condensed from the sources listed above.

The first requirement for BPA is a geographic region with at least three identifiable areas of endemism (e.g. Australia, southern South America, and New Zealand) and/or a monophyletic taxon with representatives (lineages) in at least three areas of endemism (e.g. Pilipalpinae, Nothofagus, etc.). The relationships of the groups in question must be supported by rigorous, phylogenetic analyses. From the taxon cladograms, area cladograms are produced by substituting the taxon names with the area(s) of habitation of the taxa. A matrix is then constructed, in which the rows represent the independent variables (areas of endemism), and the columns the dependent variables (taxa). The entries in the matrix are binary, with a "1" assigned if either a terminal taxon or its hypothetical ancestor can be inferred to occur, or occurred, in a particular area. A "0" is

assigned if the taxon is absent from the area. This assumes that an ancestral range is equal to the additive ranges of the descendants. The individual areas are the equivalent to taxa, and the terminal taxa and hypothetical ancestors (the latter are the syn-taxa of Kluge 1988) are the characters. The matrix can be analyzed by using PAUP, which produces the most parsimonious area relationship, based on the taxonomic group(s) analyzed.

As summarized by Kluge (1988: 318), four general types of distributional information are obtainable from groups (clades): 1) all terminal taxa are endemic (each taxon is found in only one of the recognized areas of endemism); 2) there is no representation in one of the recognized areas of endemism ('missing taxon'); 3) a terminal taxon is distributed between at least two of the areas of endemism; and 4) sympatry within a clade (two or more of the terminal taxa occur in one of the areas of endemism).

According to Kluge (1988), the first three of the above conditions are not particularly problematic for BPA. A 'missing taxon' is uninformative because it cannot be proven that the taxon is not in the area of endemism. One can predict, however, that a taxon should be found there. For many groups of animals, a collecting bias may be responsible for these missing taxa. A widespread taxon is similarly irrelevant to BPA since this taxon must either have dispersed at some time, or not responded to a vicariance event(s). Kluge (1988) suggested coding both missing and widespread taxa in a neutral manner (e.g. the "?" option in PAUP). The major problem occurs with sympatry within a clade (as in Pilipalpinae), and different authors have offered solutions to this problem. These are summarized in Wiley et al. (1991: 126). Wiley (1988a) coded sympatric members of a clade as being present in the particular area of endemism. Kluge (1988) treated areas of sympatry according to a lenient, redundancy-weighted criterion. Finally, Brooks (1990) suggested splitting areas of sympatry into individual 'subareas', and comparing the area relationships to that suggested by independent geological evidence. I have chosen here to follow Wiley (1988a).

Brooks parsimony analysis is similar to phylogenetic analysis in that both require characters and both rely variously on the criterion of parsimony. Analyses of vicariance biogeography benefit greatly from incorporation of as many individual, independent sources of data as possible. If hypothetical area relationships are supported by numerous groups of plants and animals, it adds support to this hypothesis.

The subfamily Pilipalpinae is suitable for BPA: the constituent genera are endemic, distributed among four discrete areas of endemism (AUS, CHI, NZ, MAD), and the relationships of the taxa have been analyzed phylogenetically. As stated above, BPA using only one clade is much less useful than that incorporating data from a variety of sources (monophyletic taxa). Nonetheless, BPA was performed on the Pilipalpinae to see what area relationships were supported by this particular data set. The taxon cladogram used is the one in Fig. 271, and the data matrix is given in Table 5. Sympatric areas were coded simply for presence of a taxon. For the analysis, an hypothetical ancestral area was used as the outgroup area, and the tree was rooted at this point. An exhaustive search using the DELTRAN optimization option (as suggested by Wiley (1988b) was performed, giving the following area relationships: HOL + (MAD + (NZ + (AUS + CHI))) (Fig. 272). There was a complication in that the taxon (Temnopalpus + Malagaethes) arose twice on the reconstruction, in Australia and Madagascar. Homoplasy in a character data set is easy to explain; however, a lineage originates only in one geographical area. This conflict indicates that the reconstructed phylogeny may be erroneous for (Temnopalpus + Malagaethes).

To compare the area relationships obtained from the Pilipalpinae data set with that from other groups of plants and animals, a literature search was done to select other candidate groups for BPA. In their analysis of the historical biogeography of South America, Crisci et al. (1991) identified a number of such groups. It is obvious that many groups from a diversity of higher taxa (e.g. fungi, Coniferophyta, Magnoliophyta, Annelida, Araneae, Diplopoda, Collembola, Ephemeroptera, Orthoptera, Hemiptera, Mecoptera, Hymenoptera, Diptera) show similar distributions to that of Pilipalpinae. My two criteria for

selection of groups for an extensive BPA are that the group have representatives in at least two of the areas of endemism identified for Pilipalpinae, and that a phylogenetic analysis (cladogram) is available for the group.

Analysis of groups in Crisci et al. (1991)

In their analysis of the historical biogeography of South America, Crisci et al. (1991) selected 17 taxa (each with available phylogenetic analyses) and applied three different techniques to the data. Parsimony analysis, component analysis, and quantification of component analysis were used, each with different results. Area cladograms were prepared for each monophyletic group, each of which is distributed variously among nine areas of endemism (listed below).

I used sixteen of these groups for comparison with the area relationships indicated by the reconstructed phylogeny of Pilipalpinae. These groups are [presented in the same order as in Crisci et al. (1991)]: A) Oxelytrum-Ptomaphila (Silphidae); B) Diamesinae (Chironomidae); C) Podonominae (Chironomidae); E) Elaeocarpaceae; F) Embothriinae (Proteacea); G) Metallicina (Carabidae); H) Siphlonuridae; I) Nothofagus-Fagus (Fagaceae); J) Cyttaria (Cyttariacea); K) Eriococcus-Madarococcus (Eriococcidae); L) Negria-Drepanthus (Gesneriaceae); M) Oreomyrrhis (Apiaceae); N) Drapetes (Thymelaeaceae); O) Nannochoristinae (Mecoptera); P) Drimys (Winteraceae); and Q) Aristotelia (Elaeocarpaceae). Using the original area cladograms [Fig. 1 in Crisci et al. (1991)], the terminal taxa (areas) were given numerals, and the internal nodes were given lower case letters. Each geographical area was used with each taxon, even if the taxon was absent from one or more areas. The geographical areas included in the analysis are [from Crisci et al. (1991: 153-154)]: SSA (southern South America; south of 30° S latitude and also the Andean highlands north of 30°); NSA (northern South America); AUS (Australia); NG (New Guinea); NC (New Caledonia); TAS (Tasmania); NZ (New Zealand); AF (South Africa); and NA (North America). Each group was analyzed individually using BPA, and PAUP. The pooled matrix is presented in Table 6.

Cladograms of the inferred area relationships of each of the above groups are given in Figs. 274-289. An exhaustive search of the pooled data provided five equally parsimonious trees (Figs. 290-295); the strict and majority rule consensus trees are given in Figs. 296 and 297, respectively. Among areas inhabited by Pilipalpinae, the relationships are: Tasmania + (New Zealand + (Australia + Southern South America)). In most historical biogeographical studies of Australia, Tasmania has been associated closely to mainland Australia, or at least the two have not been mentioned separately. In the analyses of the groups above, however, Tasmania forms the adelphotaxon of the remaining areas. The relationship of New Zealand, Australia and South America agree with that indicated by BPA analysis of Pilipalpinae.

Crisci et al. (1991) found that northern South America is most closely related to North America. Southern South America (Chile and adjacent western, Andean Argentina) was found to belong to a monophyletic group with Australia (including Tasmania), New Guinea, New Caledonia, and New Zealand. From the data, four conflicting views of southern South America were obtained (Crisci et al. 1991: 163): 1) southern South America as the adelphotaxon to all other austral areas; 2) southern South America as the adelphotaxon to a group including Australia, New Guinea, and New Caledonia; 3) southern South America as the adelphotaxon of New Zealand; and 4) southern South America as the adelphotaxon of Australia. Analysis of the historical biogeography of Pilipalpinae adds support for hypothesis 4 (at least when compared to the other three hypotheses).

Concluding Remarks

One can only imagine the sense of wonder, and also trepidation, experienced by Sir Joseph Dalton Hooker upon his visits to southern South America, Tasmania, and New Zealand, and upon his realization that plant taxa in these geographically isolated places

were closely related and once formed an extensive Antarctic flora. Since the days of Hooker and Darwin, many such austral disjunctions have been identified, and have attracted much attention from taxonomists and biogeographers. Other austral disjunct groups have remained obscure until relatively recently; the subfamily Pilipalpinae is an example of the latter. The underlying cause of these disjunctions has been fodder for disputes and controversies among proponents of various schools of biogeography and / or systematics generally. Regardless of which causal factor(s) are accepted, the fact that these disjunctions exist, and can be shown to exist using the principles of phylogenetic systematics, is remarkable.

One of the reasons I chose to study Pilipalpinae was their collective southern hemisphere distribution. When I began my study of genera of Pilipalpinae, I wished to analyze phylogenetically the relationships among the constituent genera, and document the corresponding geographical history of the group. However, I found that the species level classification was in need of revision, and that the actual family affinities of Pilipalpinae were not definite. Through the use of selected larval and adult structural features, I was able to develop an hypothetical evolutionary and biogeographical scenario for Pilipalpinae, and answer the basic question of family placement of Pilipalpinae. Many phylogenetically important taxa of Coleoptera, and specifically, of the salpingid group of families, are in need of this type of work. Once the individual family-level taxa are analyzed critically, the classification and evolution within the entire complex can be elucidated. Hopefully, this study of Pilipalpinae is a general model by which this can be accomplished.

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Taxon / Character	1 1 1 1 1 1 1 1 1 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8
Outgroup	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Trictenotomidae	1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Salpingidae	1 1 0 1 1 0 1 1 1 0 0 0 0 0 0 0 0 0
Boridae	1 1 0 1 1 1 0 0 0 0 1 1 1 0 0 0 0 0
Pythinae	1 1 0 1 1 1 0 0 0 1 0 0 0 0 0 0 0 1
Pilipalpinae	1 1 0 1 1 1 0 0 0 1 0 0 0 1 1 1 1 0
Pyrochroidae	1 0 0 1 1 1 0 0 0 1 0 0 0 1 0 0 1 0 1

Table 1. Character matrix from Watt (1987), with inclusion of Pyrochroidae (Pyrochroinae + Pedilinae). The rationale for character polarity is taken from pp. 117-119 in Watt (1987). Characters are listed on p. 118.

Taxon / Character	1 1 1 1 1 1 1 1 1 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8
Outgroup	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Trictenotomidae	1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Salpingidae	1 0 0 1 1 0 1 1 1 0 0 0 0 0 0 0 0 0 1
Boridae	1 1 0 1 1 1 0 0 0 0 1 1 1 0 0 0 1 0
Pythinae	1 0 0 1 0 1 0 0 0 1 0 0 0 0 0 0 0 1 1 1 1
Pilipalpinae (incl. Tydessa)	1 1 0 1 1 1 0 0 0 1 0 0 0 1 1 0 0 0 1 1
Pyrochroidae	1 0 0 1 1 1 0 0 0 1 0 0 0 0 0 ? 1 0 1 1

Table 2. Character matrix using the 18 characters listed by Watt (1987), with different interpretations for character polarities. Characters are listed on p. 118 in Watt (1987).

Taxon / Character	1 1 1 1 1 1 1 1 1 1 1 2 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0
Outgroup	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Trictenotomidae	1 ? 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0
Salpingidae	1 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1
Pythidae	1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 2 1 1
Boridae	0 1 2 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Tydessinae	0 1 0 0 0 1 1 2 1 0 1 0 0 0 0 0 0 0 0 0
Pilipalpinae	0 1 2 0 0 2 1 2 1 1 0 0 1 1 0 0 0 1 0 0
Pyrochroinae	0 1 2 0 0 2 0 1 1 1 0 0 0 0 1 1 1 1 0 0
Pedilinae	0 1 2 0 0 2 1 2 1 1 0 0 0 0 1 1 1 1 0 0

Table 3. Data matrix of 20 structural characters of larval and adults of taxa selected for their relevance to family assignment of Pilipalpinae. Character states are discussed in the text.

Taxon/char	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Tydessinae	?	2	2	0	1	0	0	1	2	2	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	?	0	0	0
Paromarteon	0	1	3	1	2	0	0	1	2	2	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	1	0	1	0	0
Temnopalpus	1	1	3	1	2	0	0	1	2	2	0	1	1	0	1	1	1	1	0	1	0	0	0	1	0	0	0	0	1	1
Malagaethes	?	?	?	1	2	0	0	1	2	2	0	1	1	0	?	?	?	?	0	?	?	0	?	1	0	0	?	?	1	1
Pilipalpus	?	?	?	1	2	0	0	1	2	2	0	1	1	0	?	1	1	1	0	?	?	1	?	1	0	0	?	0	0	0
Ranomafana	?	?	?	1	2	2	0	1	2	2	1	1	1	0	?	?	?	?	0	?	?	0	?	1	0	0	?	?	0	0
Incollogenius	?	?	?	1	2	1 2	0	1	2	2	1	1	1	1	?	1	1	1	0	?	?	0	?	1	0	0	?	0	0	0
Exocalopus	0	1	3	1	2	2	0	1	2	2	1	1	1	2	1	1	1	1	0	0	1	2	0	1	1	0	0	0	0	0
Binburrum	1	1 2	3	1	2 2	1	0	1	2	2	1	0 1	1	2	1	1	1	1	0	0	0	1	0	1	0 1	0 1	0	0	0	0
Techmessa	0	1	4	1	2	2	0	1	2	2	1	1	1	1	1	1	1	2	0	0	0	1	2	1	0	0	0	0	0	0
Techmessodes	0	1	3	1	2	2	0	1	2	2	1	1	1	2	1	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0
Cycloderus	1	1	3	1	2	2	0	1	2	2	2	1	2	2	1	1	1	1	0	0	0	1	0	1	1	0	1	1	0	0
Morpholycus	1	1	3	1	2	2	0	1	2	2	2	1	2	2	1	1	1	1	0	0	0	2	0	1	1	0	1	0	0	0
Pedilinae	0	1	1	1	2	0	1	1	2	2	0	?	0	0	0	1	0	1	0	0	0	2	0 1	0	0	0	0	0	0	0
Pyrochroinae	1	1	1	1	2	0	1	0	1	1	0	?	0	0	0	1	0	1	0	0	0	2 1	0	0	0	0	1	0	0	0

Table 4. Character matrix of 30 structural characters of larvae and adults of Tydessinae, Pilipalpinae, Pedilinae, and Pyrochroinae. Character states and polarity assessment are given in text.

Taxon/Area	HOL	MAD	NZ	CHI	AUS
a	1	1	1	1	1
Tydessinae	1	0	0	0	0
c	1	0	0	0	0
Pedilinae	1	0	0	0	0
Pyrochroinae	1	0	0	0	0
f	0	1	1	1	1
PAR	0	0	0	0	1
h	0	1	1	1	1
i	0	1	0	0	1
TEM	0	0	0	0	1
MAL	0	1	0	0	0
PIL	0	0	0	1	0
m	0	1	1	1	1
RAN	0	1	0	0	0
o	0	1	1	1	1
INC	0	1	0	0	0
q	0	0	1	1	1
r	0	0	1	1	1
TEC	0	0	1	0	0
EXO	0	0	1	0	0
u	0	0	0	1	1
BIN	0	0	0	0	1
w	0	0	0	1	1
CYC	0	0	0	1	0
MOR	0	0	0	0	1
TECH	0	0	1	0	0

Table 5. Data matrix of the inferred distributions (including hypothetical ancestral taxa) of Tydessinae, Pilipalpinae, Pedilinae and Pyrochroinae for Brooks Parsimony Analysis. HOL = Holarctic; MAD = Madagascar; NZ = New Zealand; CHI = Chile; AUS = Australia. 0 = taxon absent from area; 1 = taxon present in area. Taxon names are given in Fig. 271.

Table 6. Data matrix of the inferred distributions (including hypothetical ancestral 'taxa') of various monophyletic groups distributed in the southern hemisphere. See text for explanation of taxon and area abbreviations. 0 = taxon absent (or inferred to be absent) from area; 1 = taxon present (or inferred to be present) in area.

	Taxa																										
Area	A1	A2	A3	A4	A5	Aa	Ab	Ac	Ad	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	Ba	Bb	Bc	Bd	Be	Bf	Bg	Bh	Bi
ANC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SSA	0	1	0	1	0	1	1	1	1	0	0	0	1	0	1	0	1	0	0	1	0	1	1	1	1	1	1	0
NSA	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AUS	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1	0	1	1
NG	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TAS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1
NZ	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	1	1	1	1	0	0
AF	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
NA	0	0	0	0	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0

	Taxa																							
Area	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15	C16	C17	C18	C19	C20	C21	C22	C23	C24
ANC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SSA	0	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0	0
NSA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AUS	1	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1
NG	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TAS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NZ	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	1	1	0	1	1	0	0
AF	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NA	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0

Table 6 (continued).

	Taxa																								
Area	C25	Ca	Cb	Cc	Cd	Ce	Cf	Cg	Ch	Ci	Cj	Ck	Cl	Cm	Cn	Co	Cp	Cq	Cr	Cs	Ct	Cu	Cv	Cw	Cx
ANC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SSA	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
NSA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AUS	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	1
NG	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TAS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NZ	0	1	1	0	0	0	1	1	0	1	1	0	1	0	1	1	0	1	1	1	1	1	1	1	0
AF	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NA	0	1	1	0	0	1	1	0	0	1	0	0	1	0	1	0	0	1	0	1	1	0	1	1	0

	Taxa																											
Area	E1	E2	E3	E4	E5	E6	Ea	Eb	Ec	Ed	Ee	F1	F2	F3	F4	F5	F6	Fa	Fb	Fc	Fd	G1	G2	G3	G4	G5	G6	G7	G8
ANC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SSA	0	1	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0
NSA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1
AUS	1	0	0	0	0	1	1	1	1	1	1	0	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0
NG	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0	1	1	0	1	1	0	0	0	0	0	0	0
NC	0	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TAS	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
NZ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0

Table 6 (continued).

Area	Ga	Gb	Gc	Gd	Gd	Ge	Gf	Gg	H1	H2	H3	H4	H5	H6	H7	H8	Ha	Hb	Hc	Hd	He	Hf	Hg	I1	I2	I3	I4	I5	I6	I7	I8
ANC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SSA	1	0	1	0	0	0	0	0	1	0	0	1	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	0	1	0	0
NSA	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AUS	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0
NG	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NC	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
TAS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
NZ	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	1	1	0	0	0	1	0	0	0	0	1
AF	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NA	1	0	1	1	1	1	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0

Area	Ia	Ib	Ic	Id	J1	J2	J3	J4	J5	Ja	Jb	Jc	Jd	K1	K2	K3	K4	K5	K6	K7	Ka	Kb	Kc	Kd	Ke	Kf	L1	L2	L3	L4
ANC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SSA	1	1	1	0	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0	1	1	0	1	0	0	0
NSA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AUS	1	1	0	0	0	0	0	0	1	1	1	1	1	0	1	0	1	0	0	1	1	1	1	1	1	1	0	1	0	0
NG	1	1	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NC	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TAS	1	1	1	0	0	0	1	0	0	1	1	1	0	0	1	0	1	0	0	1	1	1	1	1	1	1	0	0	0	0
NZ	1	1	1	1	0	1	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	1	1	0	0	1	0
AF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NA	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 6 (continued).

Area	La	Lb	Lc	M1	M2	M3	M4	M5	M6	Ma	Mb	Mc	Md	Me	N1	N2	N3	N4	Na	Nb	Nc	O1	O2	O3	Oa	Ob
ANC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SSA	1	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1
NSA	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AUS	1	1	0	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1
NG	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	0	1	1	1	1	0	0	0	0	0
NC	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TAS	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	1	0	1	1	1	0	0	0	0	0
NZ	1	1	1	0	0	0	0	0	1	1	1	1	0	1	0	1	0	0	1	1	0	1	0	0	1	0
AF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Area	P1	P2	P3	P4	Pa	Pb	Pc	Q1	Q2	Q3	Q4	Qa	Qb	Qc
ANC	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SSA	1	0	0	0	1	0	0	0	0	1	0	1	0	1
NSA	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AUS	0	1	0	0	1	1	0	0	1	0	0	1	1	0
NG	0	0	1	0	1	1	1	0	0	0	0	0	0	0
NC	0	0	0	1	1	1	1	0	0	0	0	0	0	0
TAS	0	0	0	0	0	0	0	1	0	0	0	1	1	0
NZ	0	0	0	0	0	0	0	0	0	0	1	1	0	1
AF	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0

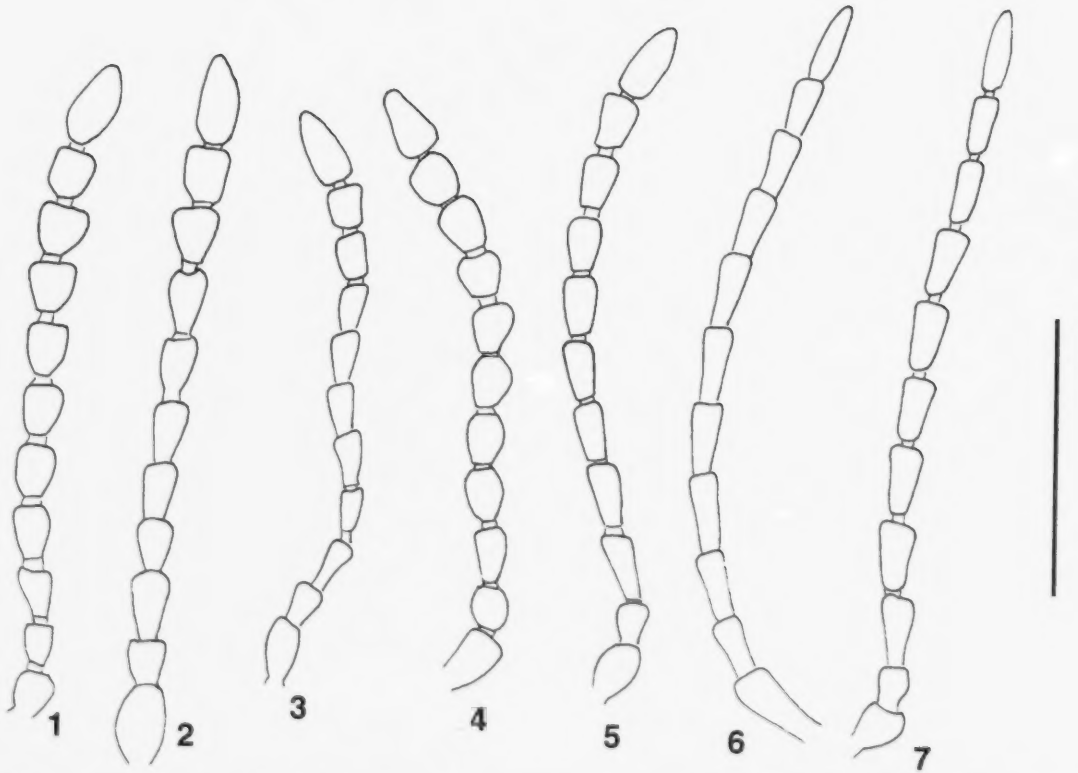


Plate 1 (Antennomeres of Pilipalpinae).—**1**. Paromarteon constans Lea. **2**. Temnopalpus niger Lea. **3**. Malagaethes lawrencei, gen. et sp. nov. **4**. Ranomafana steineri, gen. et sp. nov. **5**. Incollogenius sp. **6**. Pilipalpus dasytoides Fairmaire. **7**. Binburrum ruficollis (Champion). [Scale bar = 1.3 mm (Figs. 1, 2, 5); 1.2 mm (Fig. 3); 1.0 mm (Figs. 6, 7)]

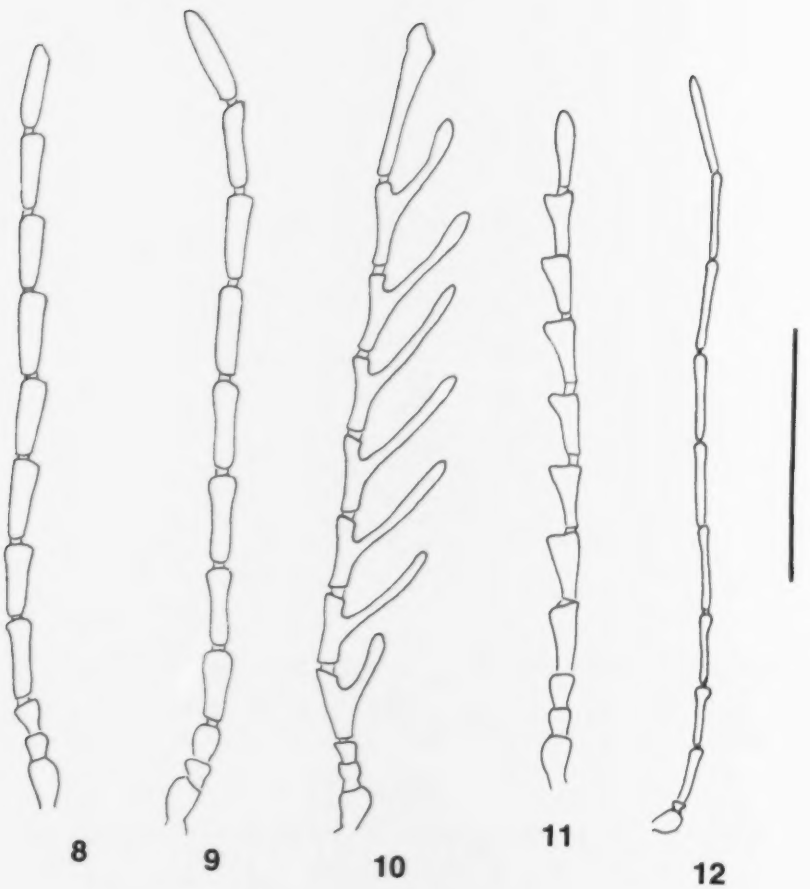


Plate 2 (Antennomeres of Pilipalpinae) .—**8**. Techmessa concolor Bates. **9**. Techmessodes versicolor Broun. **10**. Exocalopus sp. ♂. **11**. Exocalopus sp. ♀. **12**. Cycloderus immaculicollis, sp. nov. ♂. [Scale bar = 1.0 mm (Fig. 8); 0.7 mm (Figs. 9-11); 0.3 mm (Fig. 12)]

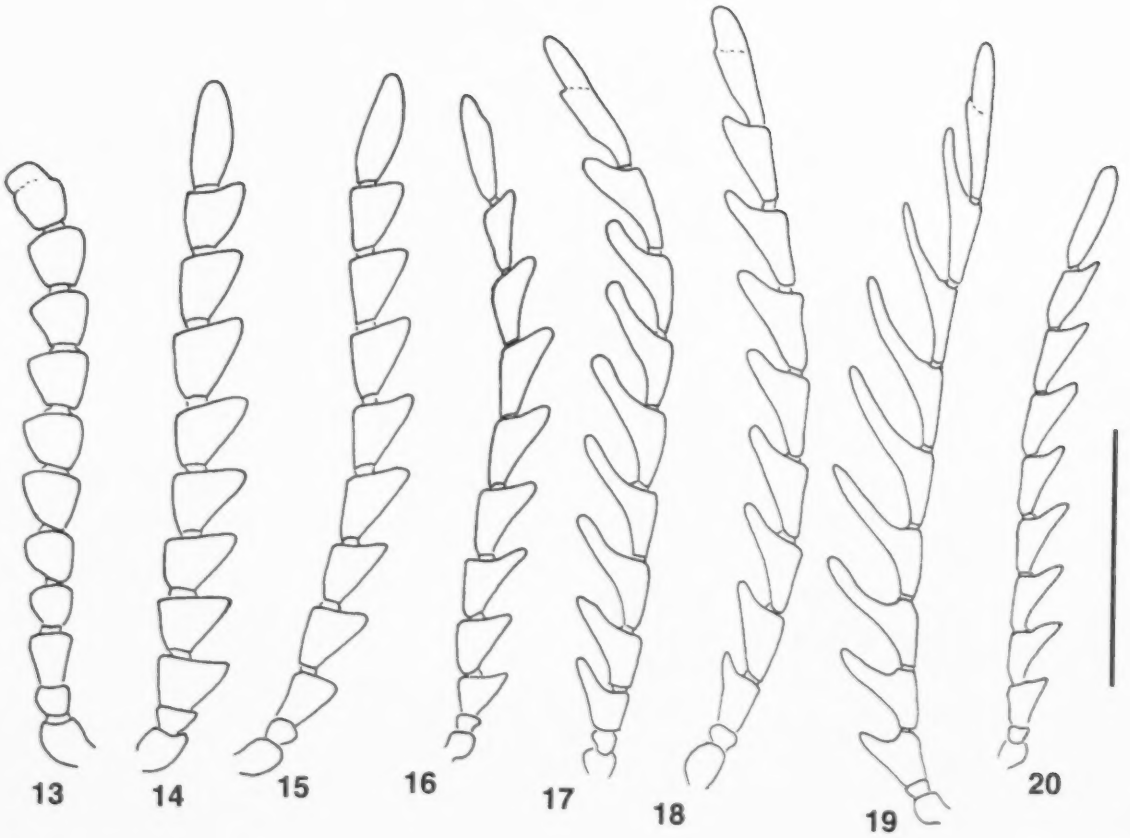


Plate 3 (Antennomeres of Morpholycus spp.).—**13**. M. monilicornis Lea. **14**. M. costipennis Lea. **15**. M. concolor (Macleay). **16**. M. nigripennis (Macleay) ♂. **17**. M. apicalis (Macleay) ♂. **18**. M. apicalis ♀. **19**. M. flabellicornis (Macleay) ♂. **20**. M. flabellicornis ♀. [Scale bar = 1.0 mm]

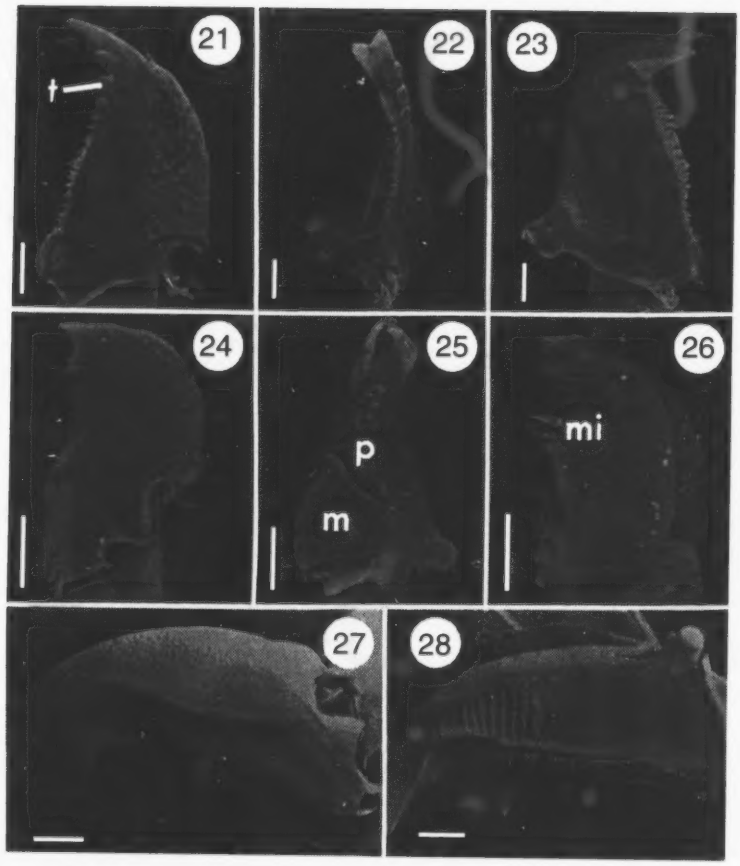


Plate 4 (adult mandibles — Pythidae and Trictenotomidae).— **21-23**. Priognathus monilicornis (Randall); 21. left dorsal. 22. right occlusal. 23. right ventral.—**24-26**. Sphalma quadricollis Horn. 24. right dorsal. 25. left occlusal. 26. left ventral.—**27-28**. Trictenotoma sp. 27. right dorsal. 28. left ventral. m = mola; mi = microtrichia; p = prostheca; t = terebral tooth [Scale bar = 0.1 mm (Figs. 21-23), 0.2 mm (Figs. 24-26), 1.0 mm (Figs. 27-28)]

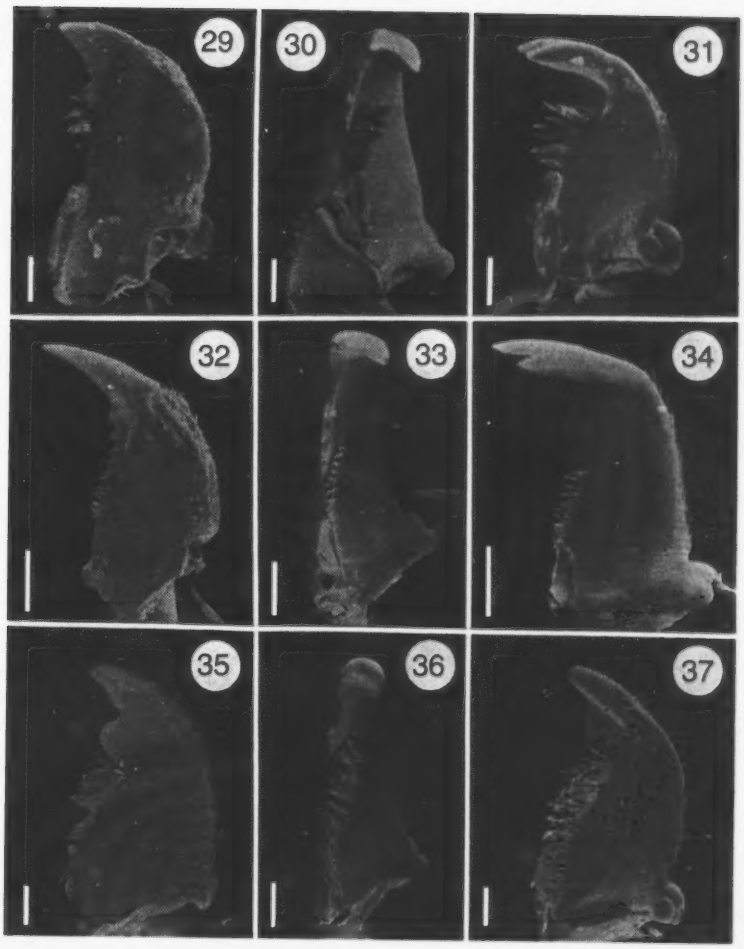


Plate 5 (adult mandibles — Boridae).—**29-31**. Boros unicolor Say. 29. right dorsal. 30. left occlusal. 31. left ventral.—**32-34**. Lecontia discicollis (LeConte). 32. right dorsal. 33. left occlusal. 34. left ventral.—**35-37**. Synercticus heteromerus Newman. 35. right dorsal. 36. left occlusal. 37. left ventral. [Scale bar = 0.1 mm (Figs. 29-31, 35-37), 0.4 mm (Figs. 32-34)]

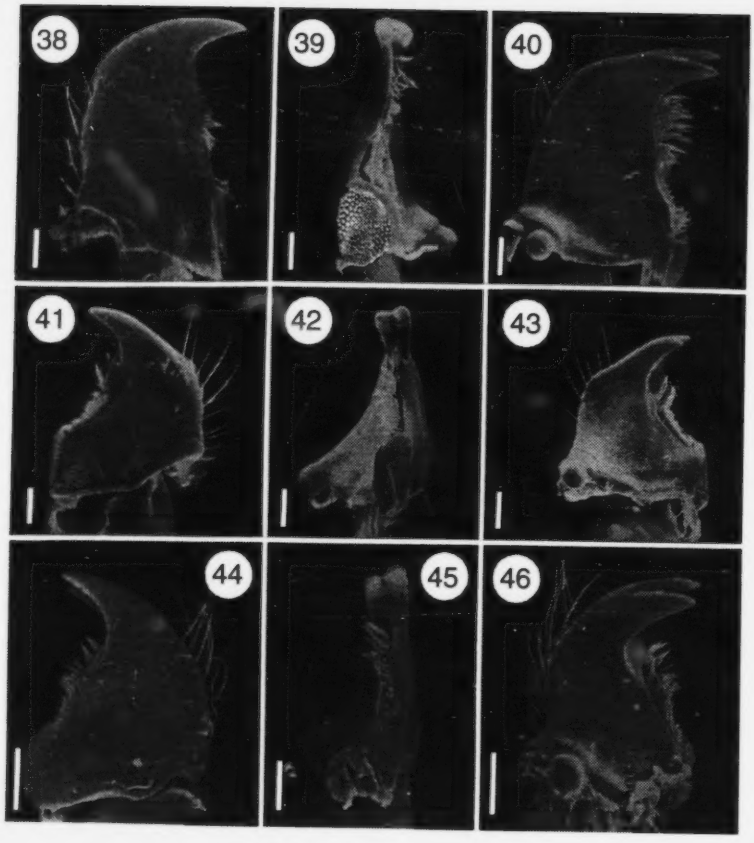


Plate 6 (adult mandibles — Pilipalpinae 1).—**38-40**. Paromarteon apicale Lea. 38. left dorsal. 39. left occlusal. 40. right ventral.—**41-43**. Temnopalpus niger Lea. 41. right dorsal. 42. right occlusal. 43. right ventral.—**44-46**. Pilipalpus dasytoides Fairmaire. 44. right dorsal. 45. right occlusal. 46. right ventral. [Scale bar = 0.04 mm (Figs. 38-43), 0.08 mm (Figs. 44-46)]

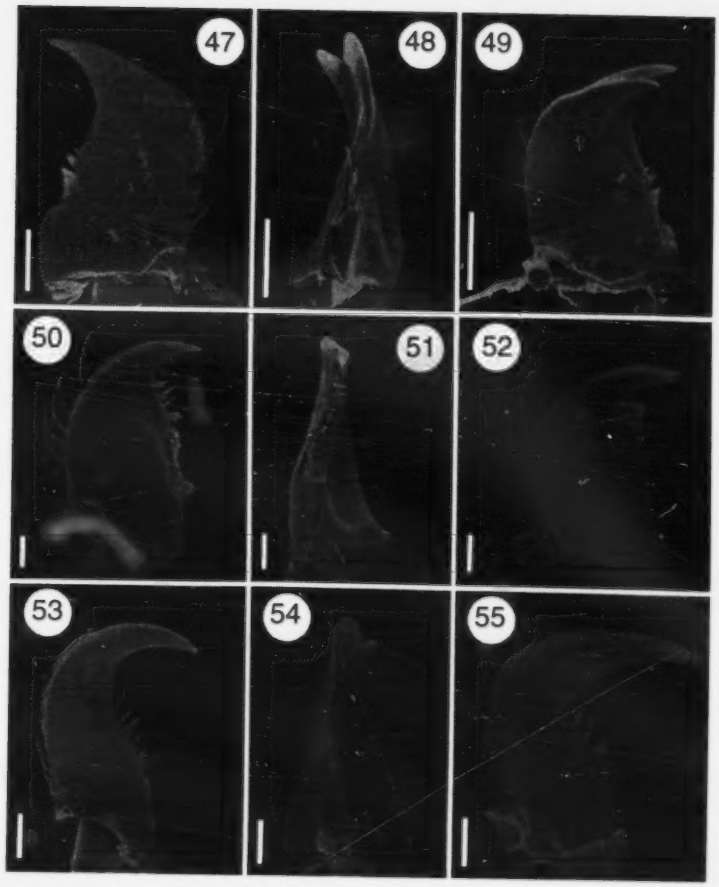


Plate 7 (adult mandibles — Pilipalpinae 2).–**47-49**. Incollogenius sp. 47. right dorsal. 48. right occlusal. 49. right ventral.—**50-52**. Binburrum concavifrons, gen. et sp. nov. 50. left dorsal. 51. left occlusal. 52. right ventral. **53-55**. Techmessa concolor Bates. 53. left dorsal. 54. left occlusal. 55. right ventral. [Scale bar = 0.04 mm (Figs. 50-52), 0.1 mm (Figs. 47-49, 53-55)]

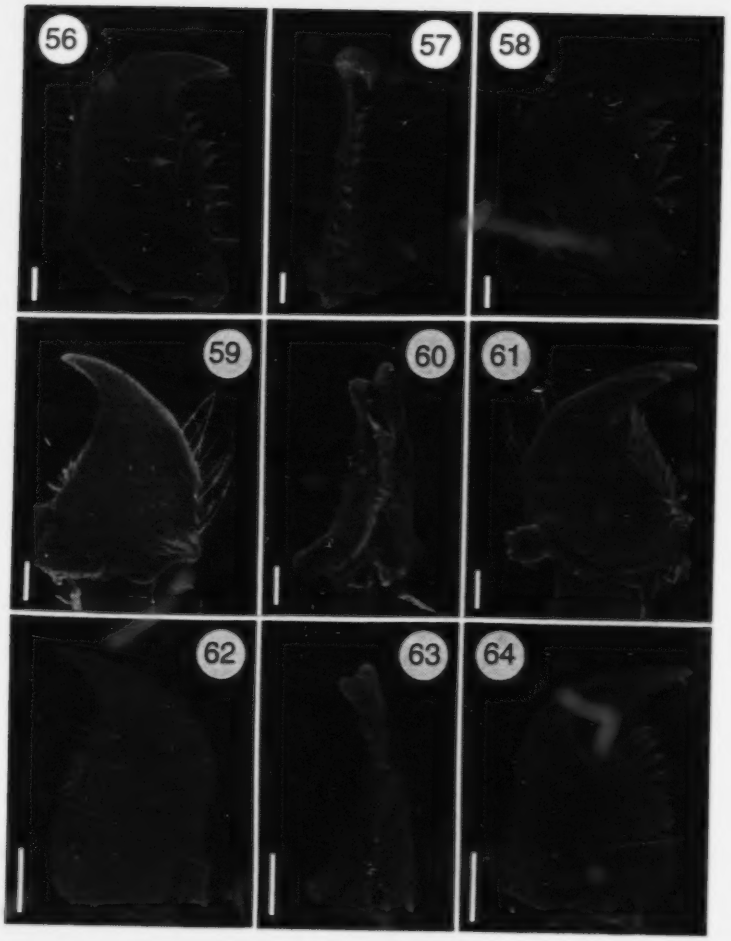


Plate 8 (adult mandibles — Pilipalpinae 3).—**56-58**. Techmessodes picticornis (Broun). 56. left dorsal. 57. left occlusal. 58. right ventral. —**59-61**. Exocalopus sp. 59. right dorsal. 60. right occlusal. 61. right ventral.—**62-64**. Cycloderus rubricollis Solier. 62. right dorsal. 63. right occlusal. 64. right ventral. [Scale bar = 0.04 mm (Figs. 56-61), 0.1 mm (Figs. 62-64)]

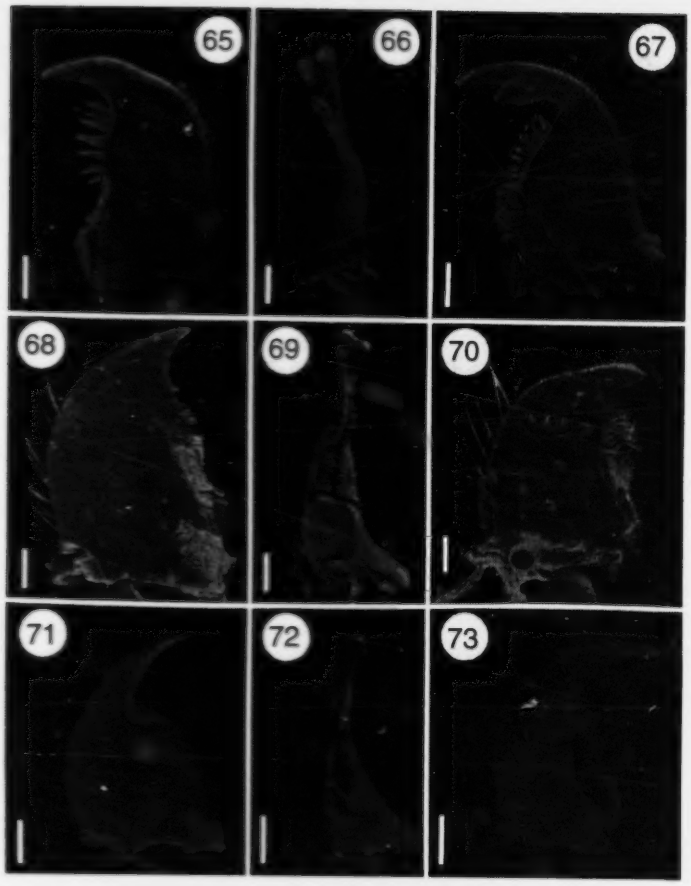


Plate 9 (adult mandibles — Pilipalpinae, Tydessinae, Pedilinae). —**65-67**. Morpholycus costipennis Lea. 65. right dorsal. 66. right occlusal. 67. left ventral.—**68-70**. Tydessa blaisdelli Pollock. 68. left dorsal. 69. left occlusal. 70. right ventral.—**71-73**. Pedilus joanae Young. 71. left dorsal. 72. left occlusal. 73. right ventral. [Scale bar = 0.1 mm (Figs. 65-67, 71-73), 0.04 mm (Figs. 68-70)]

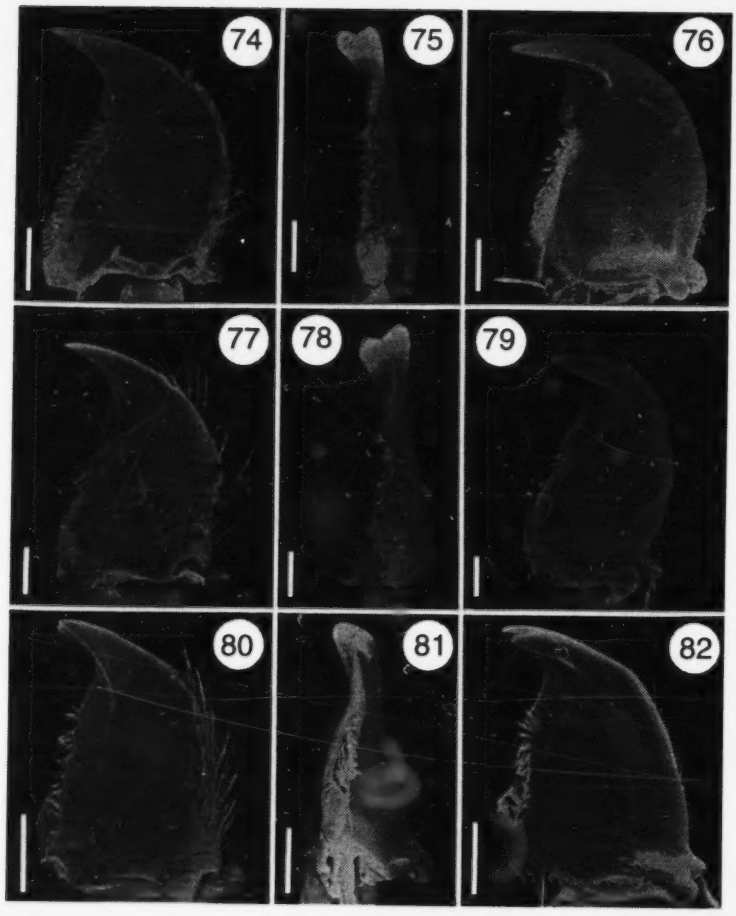


Plate 10 (adult mandibles — Pyrochroinae).—**74-76**. Neopyrochroa flabellata (Fabr.). 74. right dorsal. 75. right occlusal. 76. left ventral. —**77-79.** Dendroides canadensis Latr. 77. right dorsal. 78. right occlusal. 79. left ventral.—**80-82**. Schizotus pectinicornis(L.). 80. right dorsal. 81. left occlusal. 82. left ventral. [Scale bar = 0.2 mm (Figs. 74-76), 0.1 mm (Figs. 77-82)]

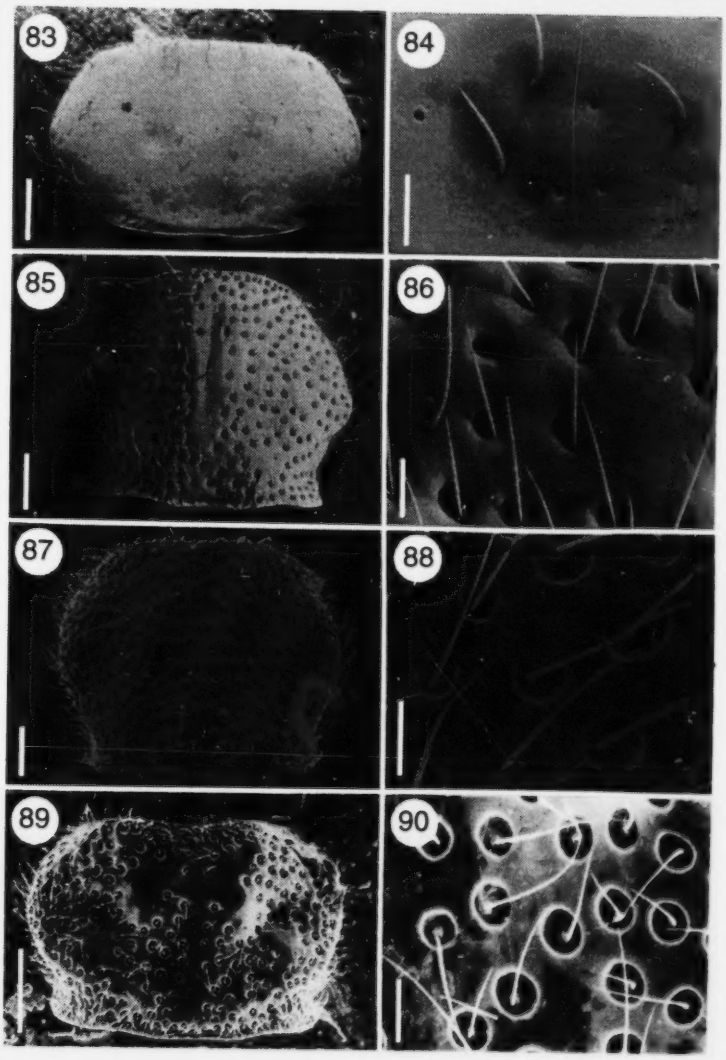


Plate 11 (pronotum and detail of punctation — Pilipalpinae 1).–**83-84**. Paromarteon apicale Lea. **85-86**. Binburrum concavifrons, gen. et sp. nov. **87-88**. Techmessa concolor Bates. **89-90**. Exocalopus sp. [Scale bar = 0.2 mm (Figs. 83, 85, 87, 89), 0.04 mm (Figs. 84, 86, 88, 90)]

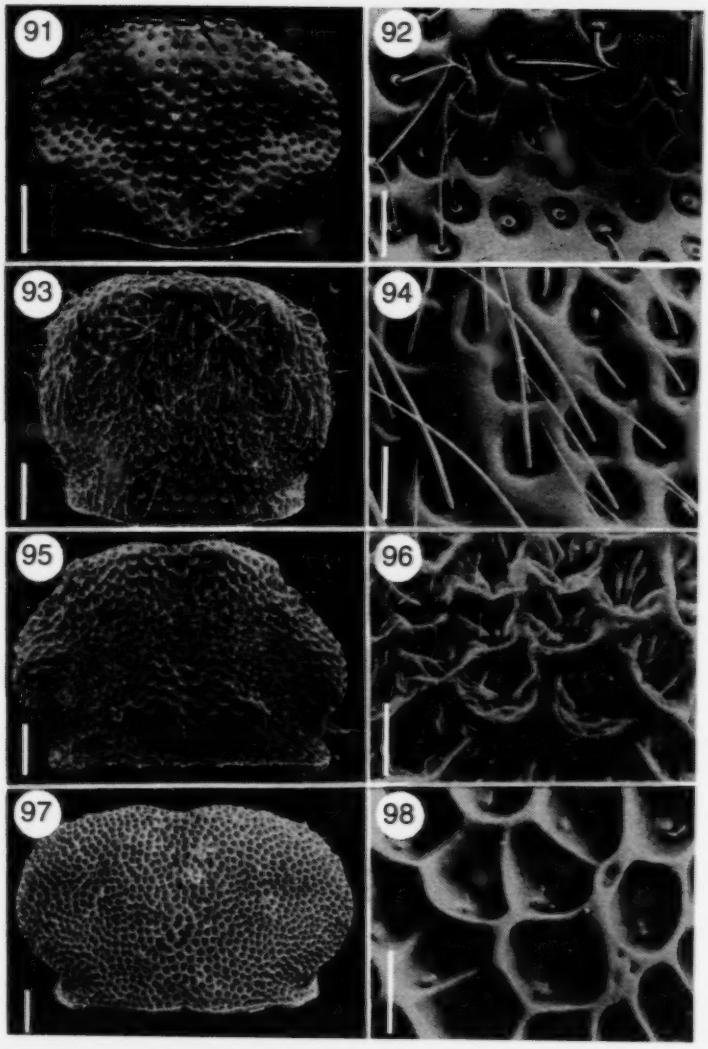


Plate 12 (pronotum and detail of punctation — Pilipalpinae 2).— **91-92**. Techmessodes picticornis (Broun). **93-94**. Cycloderus hirsutus, sp. nov. **95-96**. C. magellanicus Philippi. 97-98. C. planipennis Fairm. and Germain. [Scale bar = 0.2 mm (Figs. 91, 93, 95, 97), 0.04 mm (Figs. 92, 94, 96, 98)]

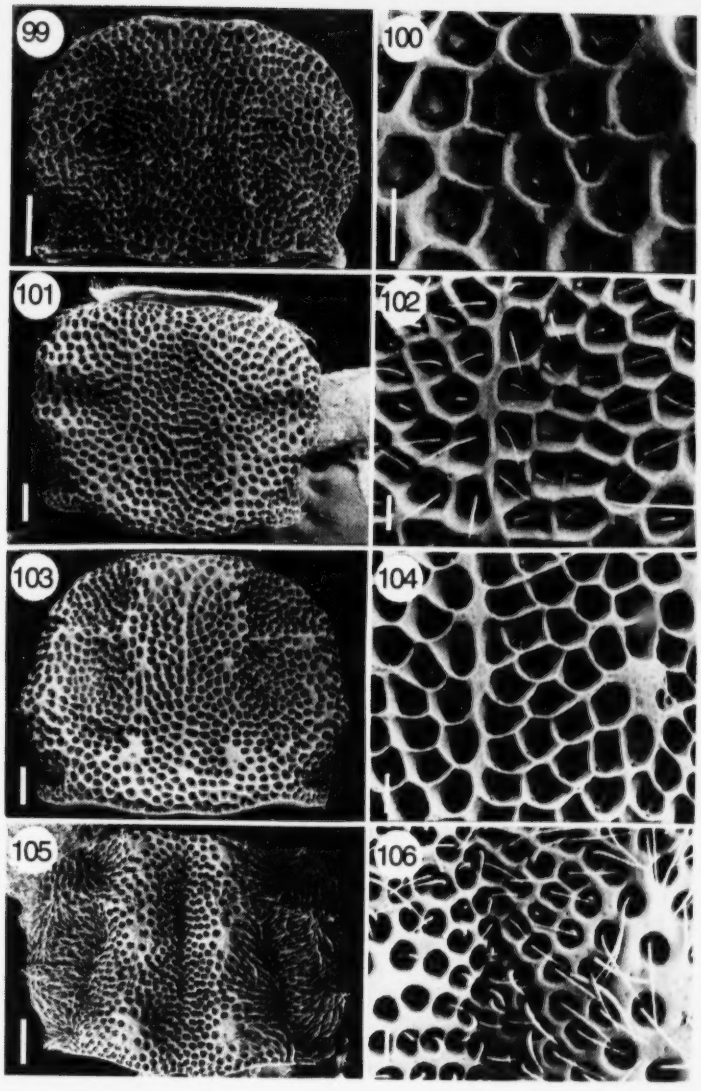


Plate 13 (pronotum and detail of punctation — Pilipalpinae 3).–**99-100**. Cycloderus signaticollis Fairm. and Germain. **101-102**. Morpholycus monilicornis Lea. **103-104**. M. costipennis Lea. **105-106**. M. apicalis (Macleay). [Scale bar = 0.2 mm (Figs. 99, 101, 103, 105), 0.04 mm (Figs. 100, 102, 104, 106)]

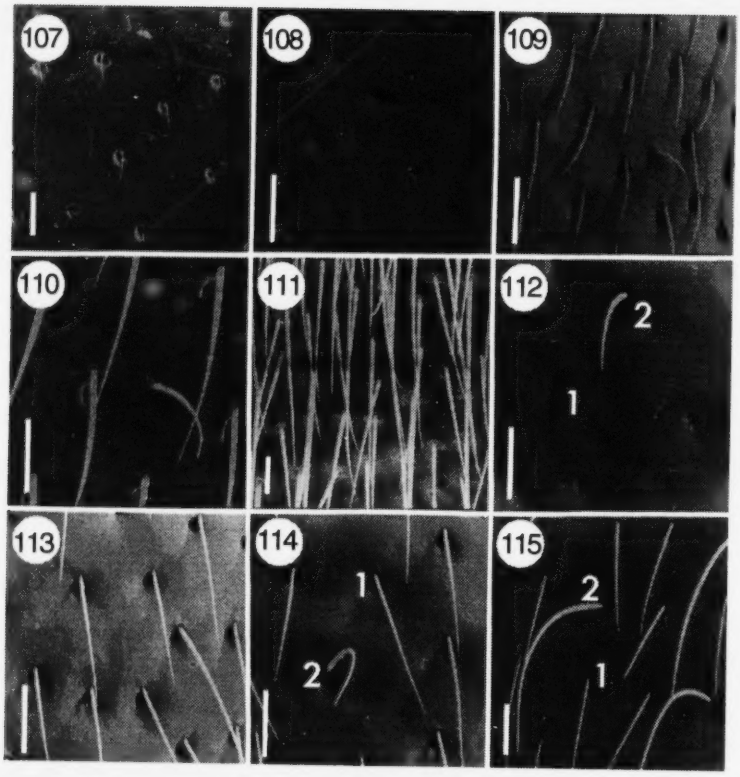


Plate 14 Elytral punctation detail — Boridae, Tydessinae, Pedilinae, Pyrochroinae, Pilipalpinae.—**107**. Boros unicolor Say. **108**. Tydessa blaisdelli Pollock. **109**. Tydessa lewisi (Pic). **110**. Pedilus joanae Young. **111**. Neopyrochroa flabellata(Fabr.). **112**. Paromarteon apicale Lea. **113**. Temnopalpus bicolor Blackburn. **114**. Temnopalpus niger Lea. **115**. Pilipalpus dasytoides Fairmaire. 1 = primary elytral puncture / seta; 2 = secondary elytral puncture / seta [Scale bar = 0.04 mm]

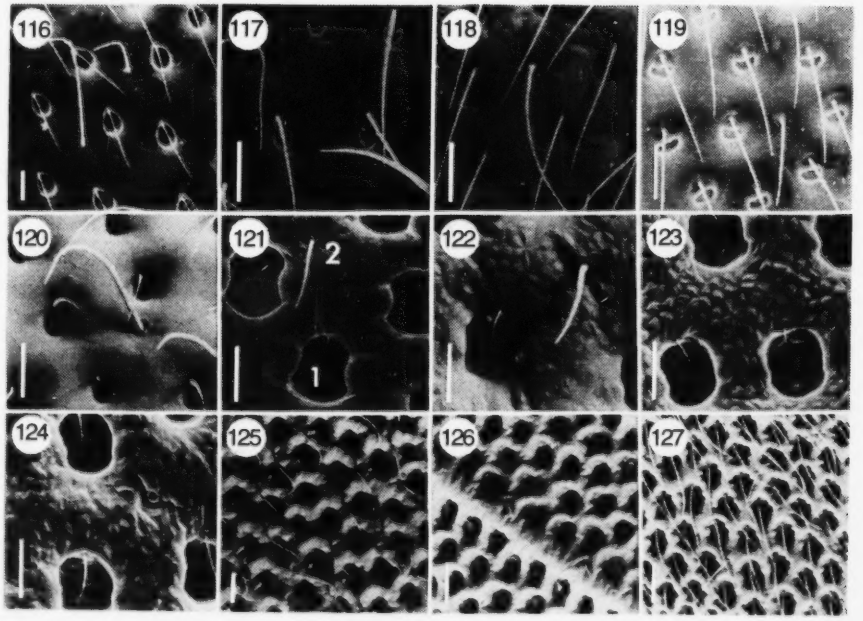


Plate 15 (elytral punctation detail — Pilipalpinae).—**116**. Binburrum concavifrons, gen. et sp. nov. **117**. Techmessa concolor Bates. **118**. Techmessodes picticornis (Broun). **119**. Exocalopus sp. **120**. Cycloderus hirsutus, sp. nov. **121**. C. rubricollis Solier. 122. C. magellanicus Philippi. **123**. C. signaticollis Fairm. and Germain. **124**. C. planipennis Fairm. and Germain. **125**. Morpholycus monilicornis Lea. **126**. M. costipennis Lea. **127**. M. apicalis (Macleay). 1 = primary elytral puncture / seta; 2 = secondary elytral puncture / seta [Scale bar = 0.04 mm]

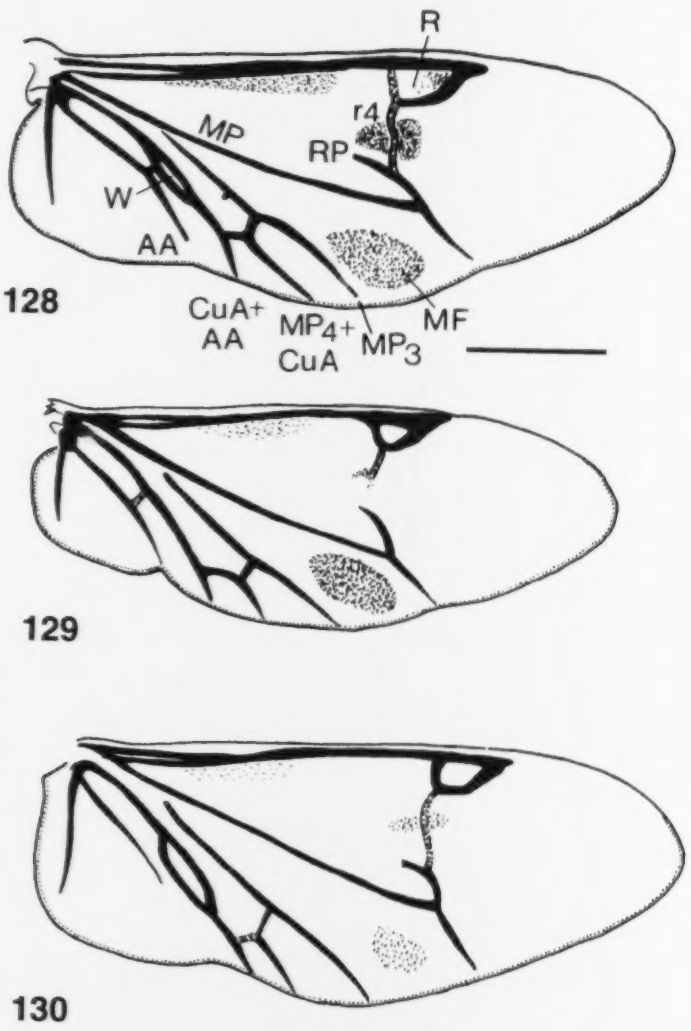


Plate 16 (flight wings of representative Pilipalpinae).—**128**. Paromarteon apicale Lea. **129**. Temnopalpus bicolor Blackburn. **130**. Pilipalpus dasytoides Fairmaire. AA = anal anterior; CuA = cubitus anterior; MF = medial fleck; MP = media posterior; r4 = radial cross-vein; R = radial cell; RP = radius posterior; W = wedge cell [Scale bar = 1.0 mm (Figs. 128-129); 0.8 mm (Fig. 130)]

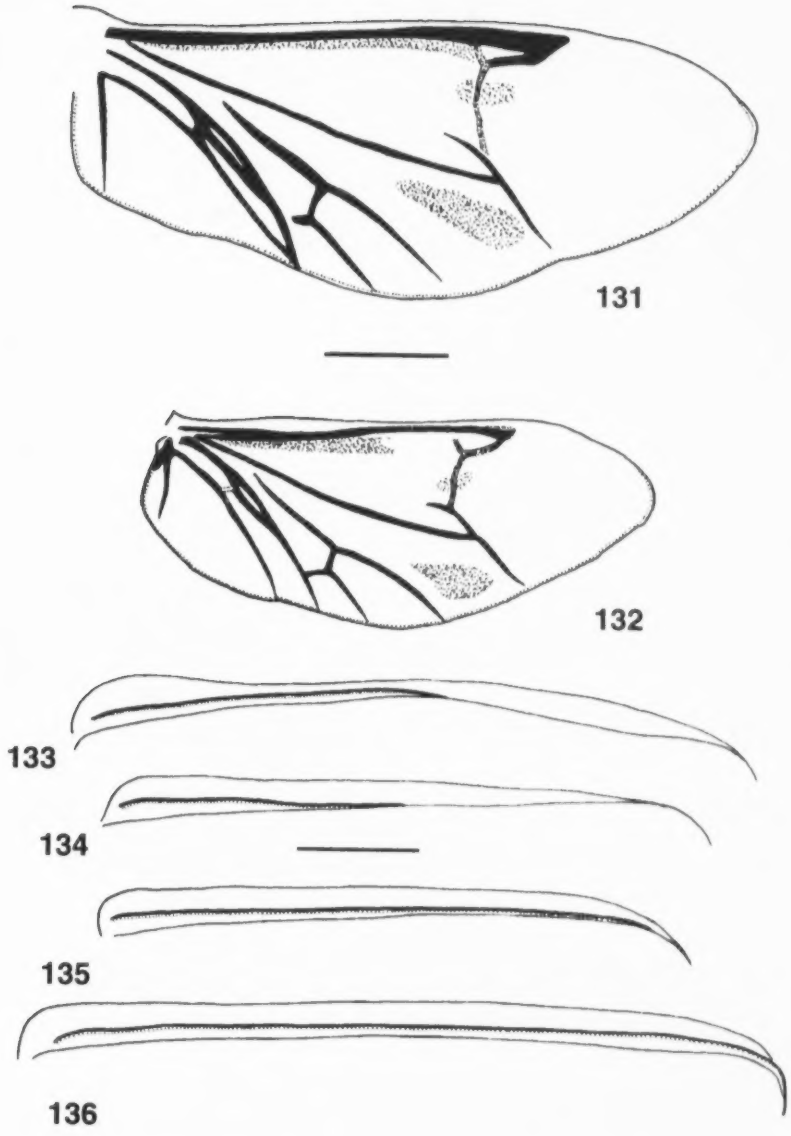


Plate 17 (flight wings and epipleura of representative Pilipalpinae).—**131**. Binburrum ruficollis (Champion). **132**. Cycloderus rubricollis Solier. **133**. Paromarteon mutabile Blackburn. **134**. Temnopalpus bicolor Blackburn. **135**. Binburrum concavifrons, sp. nov. **136**. Morpholycus monilicornis. [Scale bar = 1.0 mm (Figs. 135-136); 2.0 mm (Fig. 133); 1.7 mm (Fig. 134)]

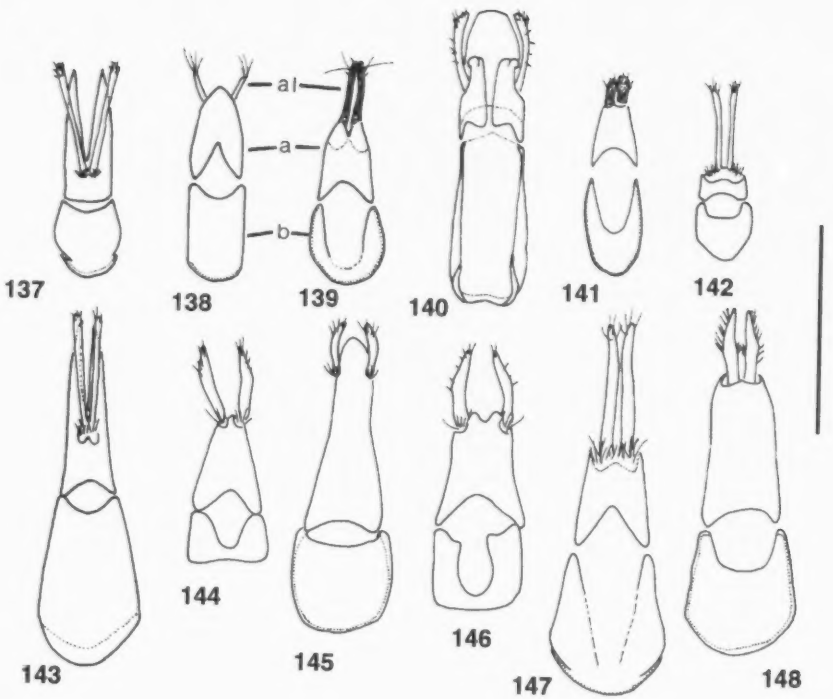


Plate 18 (male genitalia of Pilipalpinae, median lobe removed).—**137**. Paromarteon apicale Lea. **138**. Temnopalpus niger Lea. **139**. Malagaethes lawrencei, gen. et sp. nov. **140**. Pilipalpus dasytoides Fairmaire. **141**. Ranomafana steineri, gen. et sp. nov. **142**. Incollogenius sp. **143**. Binburrum concavifrons, gen. et sp. nov. **144**. Exocalopus sp. **145**. Techmessa concolor Bates. **146**. Techmessodes picticornis (Broun). **147**. Cycloderus immaculicollis, sp. nov. a = apicale; al = accessory lobes; b = basale [Scale bar = 1.0 mm (Figs. 137, 140, 141, 142, 143, 145, 147); 0.6 mm (Fig. 138); 0.8 mm (Figs. 139, 144, 146); 1.2 mm (Fig. 148)]

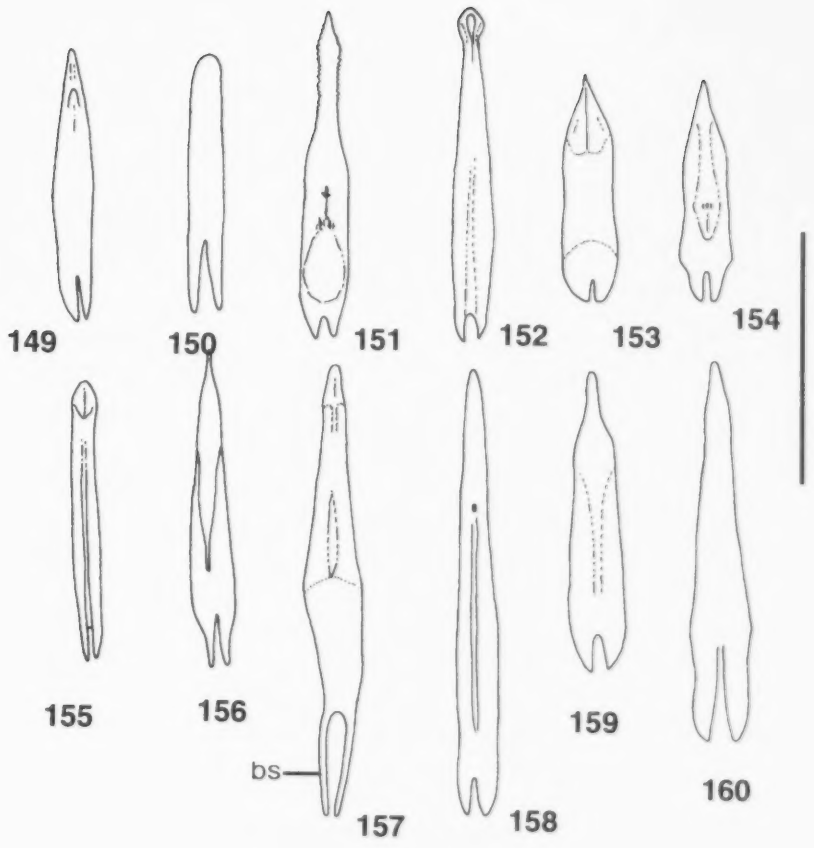


Plate 19 (median lobes of Pilipalpinae).—**149**. Paromarteon apicale Lea. **150**. Temnopalpus niger Lea. **151**. Malagaethes lawrencei, gen. et sp. nov. **152**. Pilipalpus dasytoides Fairmaire. **153**. Ranomafana steineri, gen. et sp. nov. **154**. Incollogenius sp. **155**. Binburrum angusticollis, gen. et sp. nov. **156**. Exocalopus sp. **157**. Techmessa concolor Bates. **158**. Techmessodes picticornis (Broun). **159**. Cycloderus rubricollis Solier. **160**. Morpholycus monilicornis. bs = basal strut [Scale bar = 1.0 mm (Figs. 149, 152-154, 155, 157, 159); 0.6 mm (Fig. 150); 0.8 mm (Figs. 151, 156, 158); 1.2 mm (Fig. 160)]

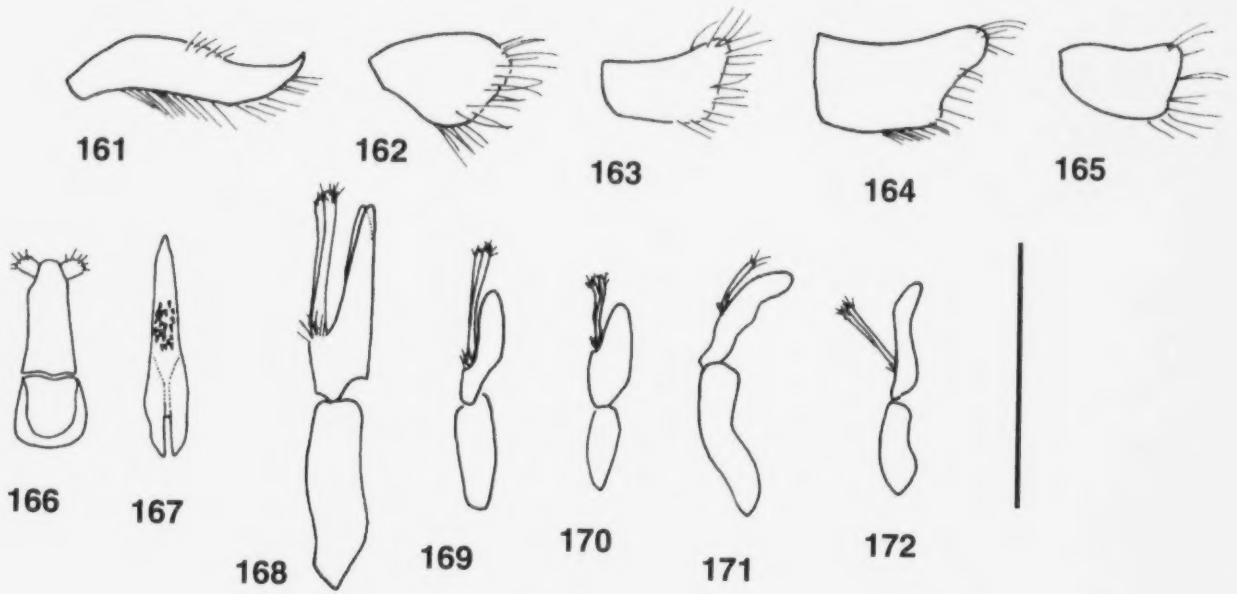


Plate 20 (male genitalia, miscellaneous).—161-165. Accessory lobes of Morpholycus species. **161**. M. monilicornis Lea. **162**. M. costipennis Lea. **163**. M. nigripennis (Macleay). **164**. M. apicalis (Macleay). **165**. M. flabellicornis (Macleay). **166**. Tegmen of Techmessodes versicolor Broun (ventral). **167**. Median lobe of Techmessodes versicolor Broun.—168-172. Tegmena of Binburrum, gen. nov. (lateral). **168**. B. concavifrons, sp. nov. **169**. B. ruficollis (Champion). **170**. B. bifoveicollis (Lea). **171**. B. angusticollis, sp. nov. **172**. B. ephippiatum (Wilson). [Scale bar = 1.0 mm (Figs. 166-172); 0.7 mm (Figs. 161-165)]

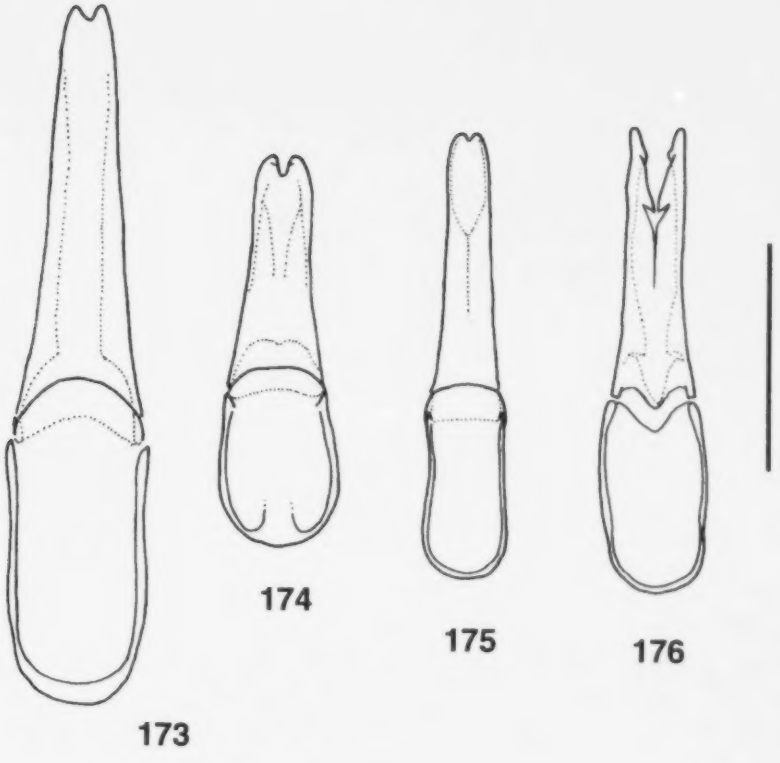


Plate 21 (male genitalia of Pyrochroinae and Pedilinae, median lobe removed).— **173**. Pyrochroa coccinea (L.). **174**. Neopyrochroa flabellata (Fabr.). **175**. Dendroides canadensis Latr. **176**. Pedilus sp. [Scale bar = 1.0 mm (Figs. 173, 175-176); 2.0 mm (Fig. 174)]

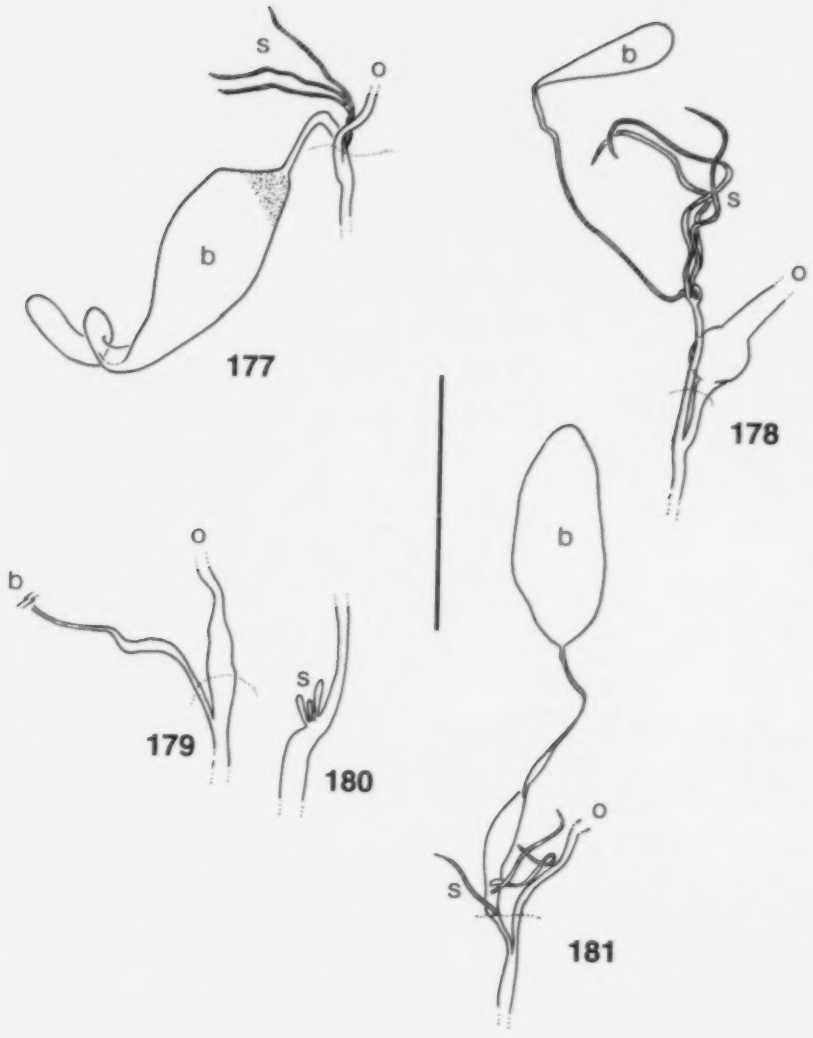


Plate 22 (internal female reproductive tract of representative Pilipalpinae).— **177**. Paromarteon apicale Lea. **178**. Temnopalpus niger Lea. **179**. Pilipalpus dasytoides Fairmaire (bursa not shown in drawing). **180**. ditto, detail of spermatheca(e). **181**. Incollogenius sp. b = bursa copulatrix; o = oviduct; s = spermatheca(e) [Scale bar = 1.0 mm (Figs. 177-179); 1.3 mm (Fig. 181)]

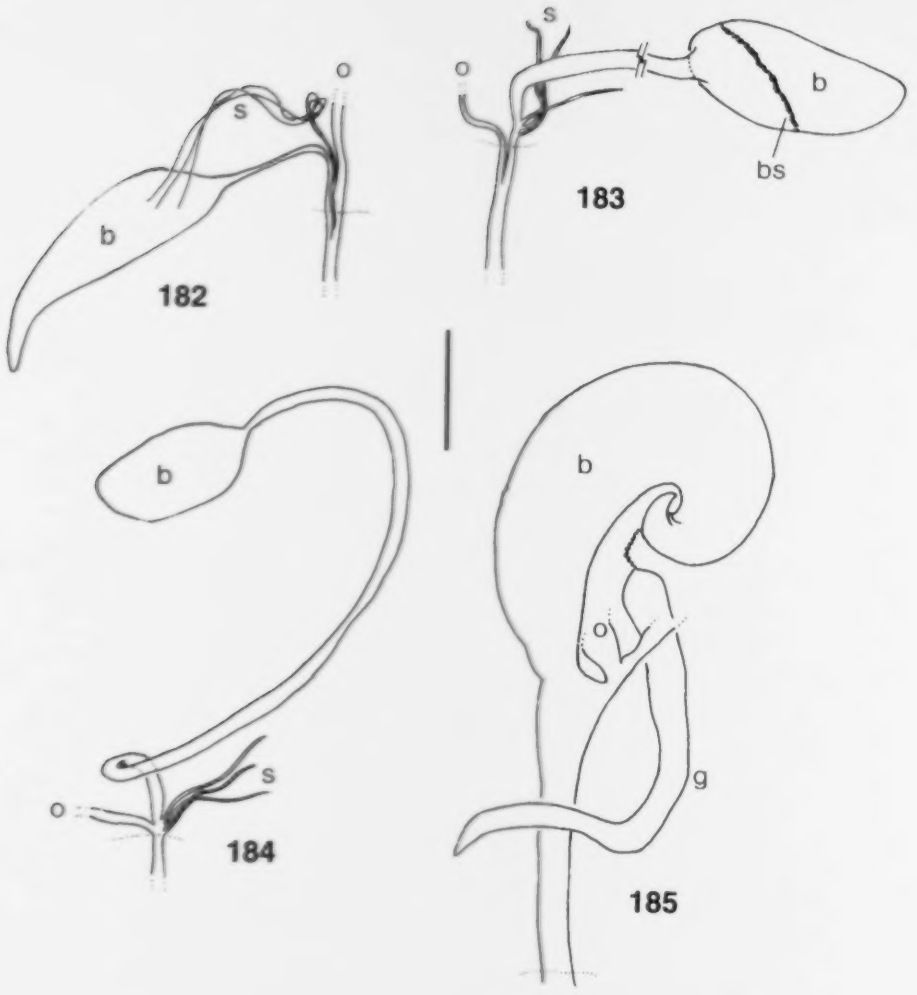


Plate 23 (internal female reproductive tract of representative Pilipalpinae and Boridae).—**182**. Binburrum ruficollis (Champion). **183**. Cycloderus rubricollis Solier. **184**. Morpholycus monilicornis Lea. **185**. Lecontia discicollis (LeC.). b = bursa copulatrix; g = gland; o = oviduct; s = spermatheca(e) [Scale bar = 1.0 mm (Figs. 183-185); 0.6 mm (Fig. 182)]

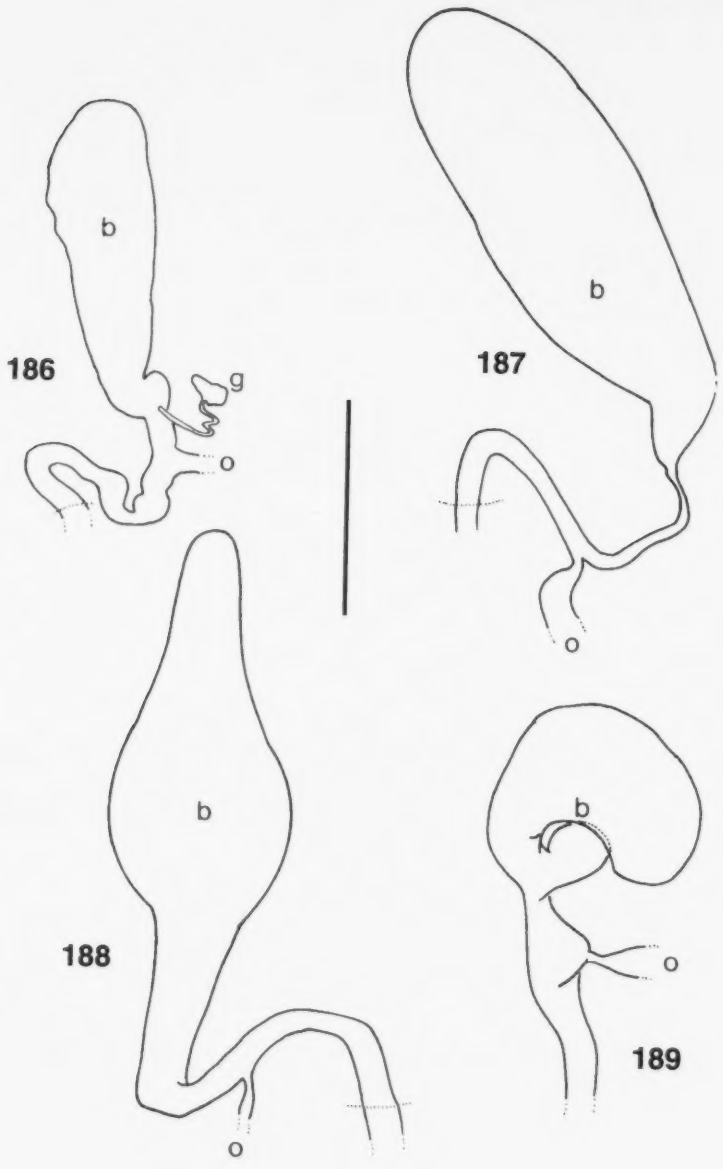


Plate 24. (internal female genitalia of representative Pyrochroinae, Pedilinae and Pythidae).—**186**. Tydessa blaisdelli Pollock. **187**. Pyrochroa coccinea (L.). **188**. Pedilus joanae Young. **189**. Pytho niger Kby. b = bursa copulatrix; g = gland; o = oviduct [Scale bar = 1.0 mm (Figs. 186, 188); 2.3 mm (Fig. 187); 0.6 mm (Fig. 189)]

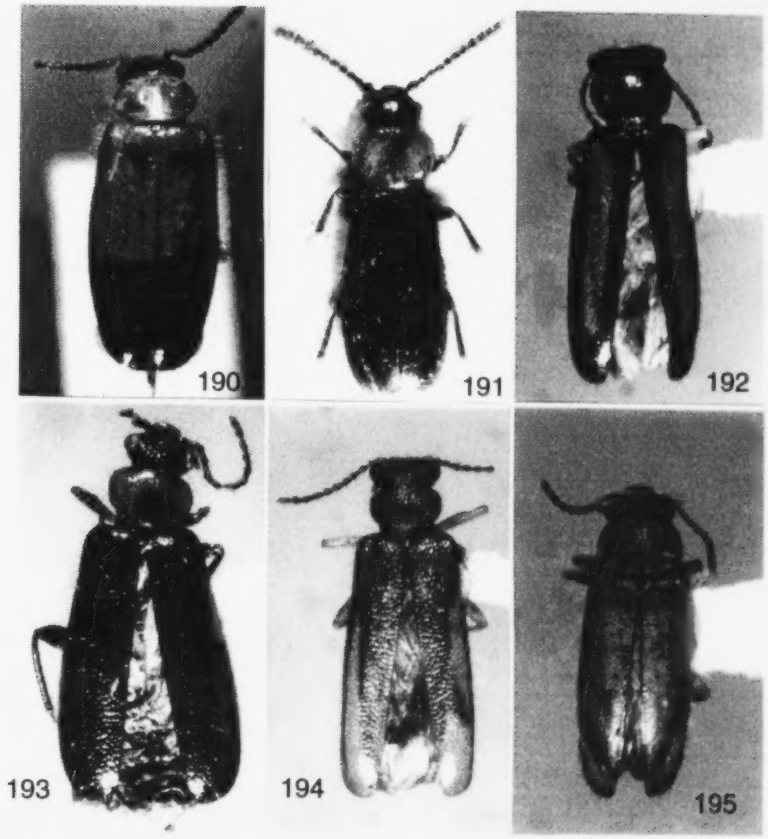


Plate 25 (Adult habitus 1) —**190**. Paromarteon apicale Lea ♂. **191**. Temnopalpus bicolor Blackburn. **192**. Malagaethes lawrencei, gen. et sp. nov. ♂. **193**. Pilipalpus dasytoides Fairmaire (maculate form) ♀. **194**. Incollogenius sp. ♂ **195**. Ranomafana steineri, gen. et sp. nov. ♂.

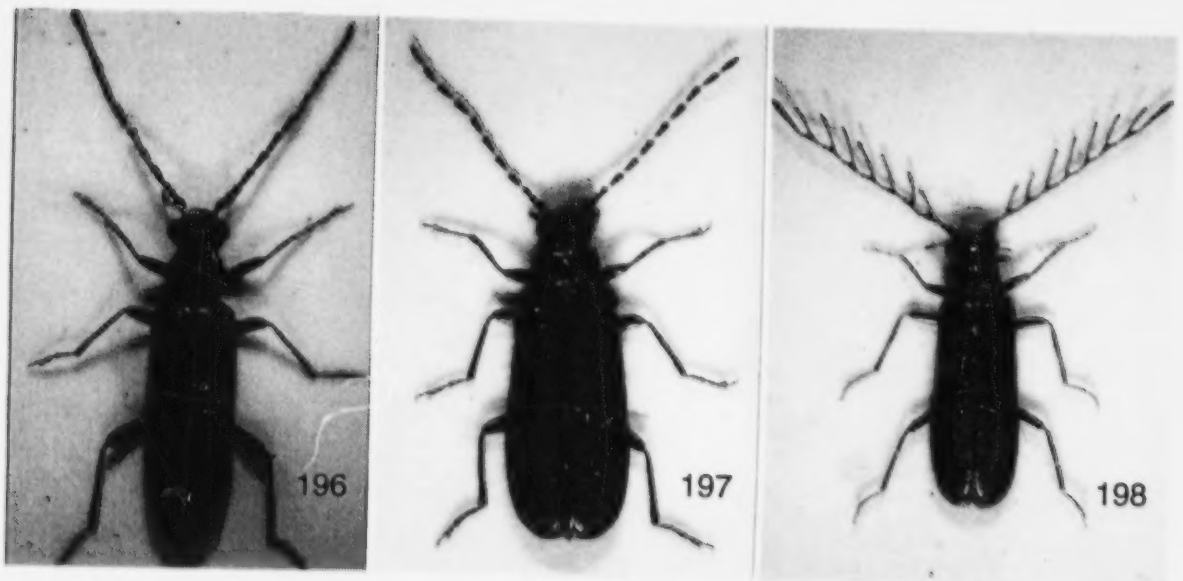


Plate 26 (Adult habitus 2).—**196**. Techmessa concolor Bates ♂. **197**. Techmessodes picticornis (Broun). **198**. Exocalopus sp. ♂.

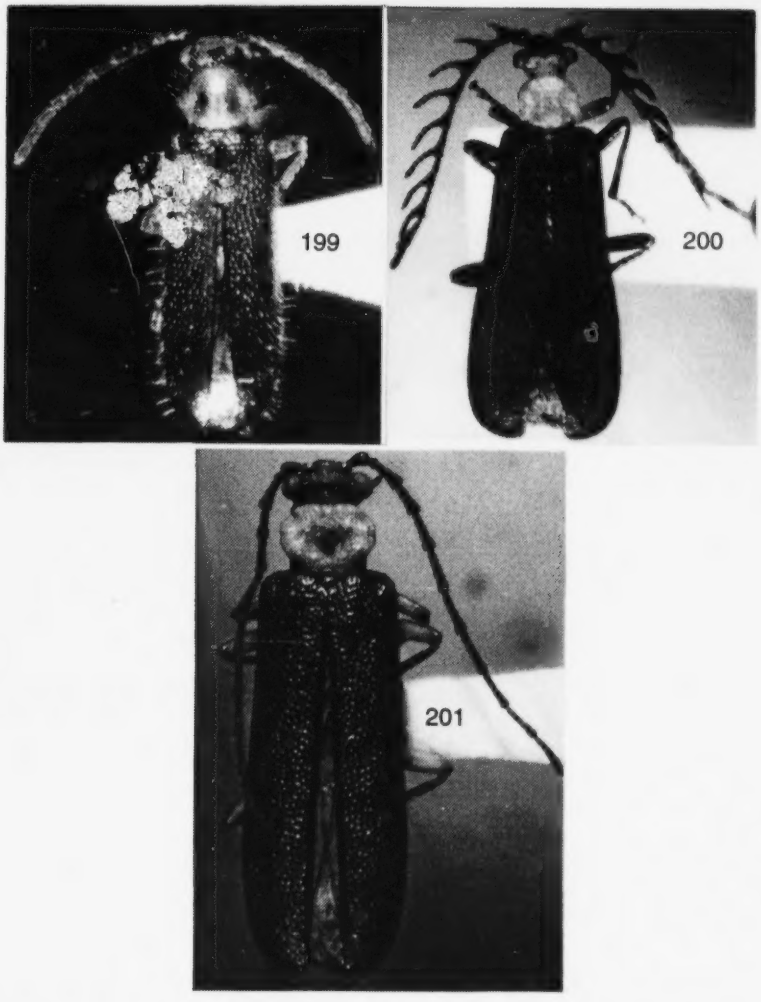


Plate 27 (Adult habitus 3). —**199**. Binburrum concavifrons, gen. et sp. nov. ♂. **200**. Morpholycus flabellicornis (Macleay) ♂. **201**. Cycloderus rubricollis Solier ♂.

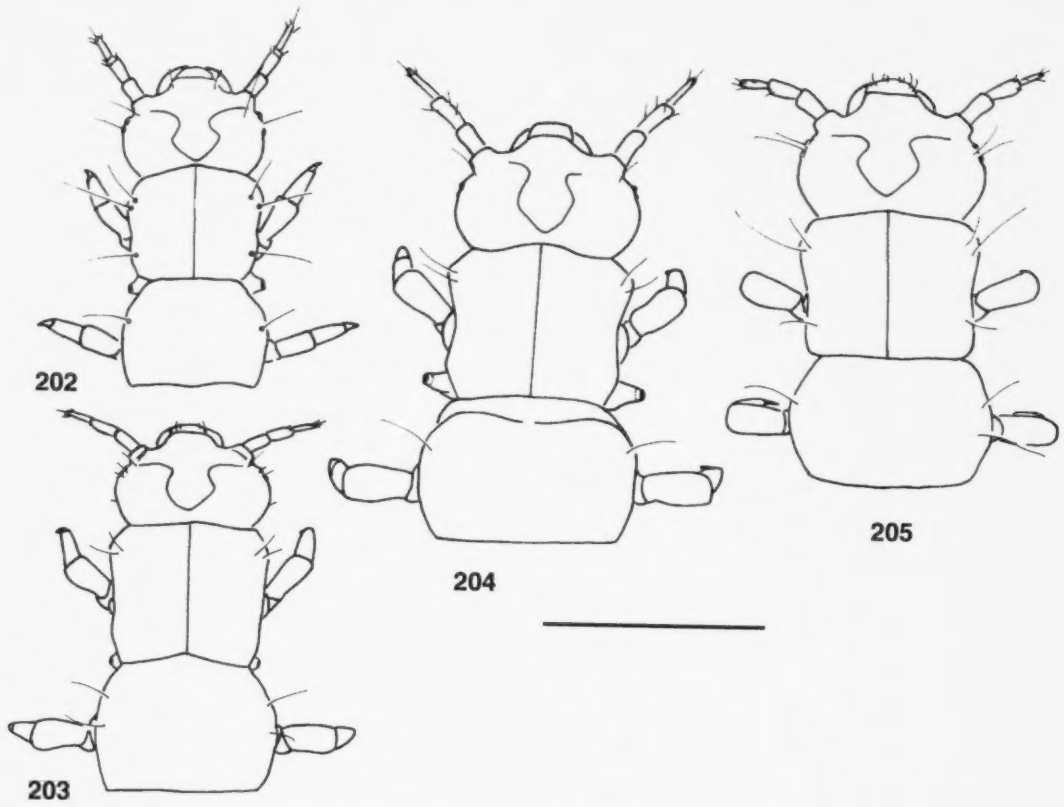


Plate 28 (larval forebodies 1).—**202**. Paromarteon sp. **203**. Temnopalpus sp. **204**. Binburrum sp. **205**. Techmessodes sp. [Scale bar = 1.0 mm (Figs. 202, 204), 1.3 mm (Figs. 203, 205)]

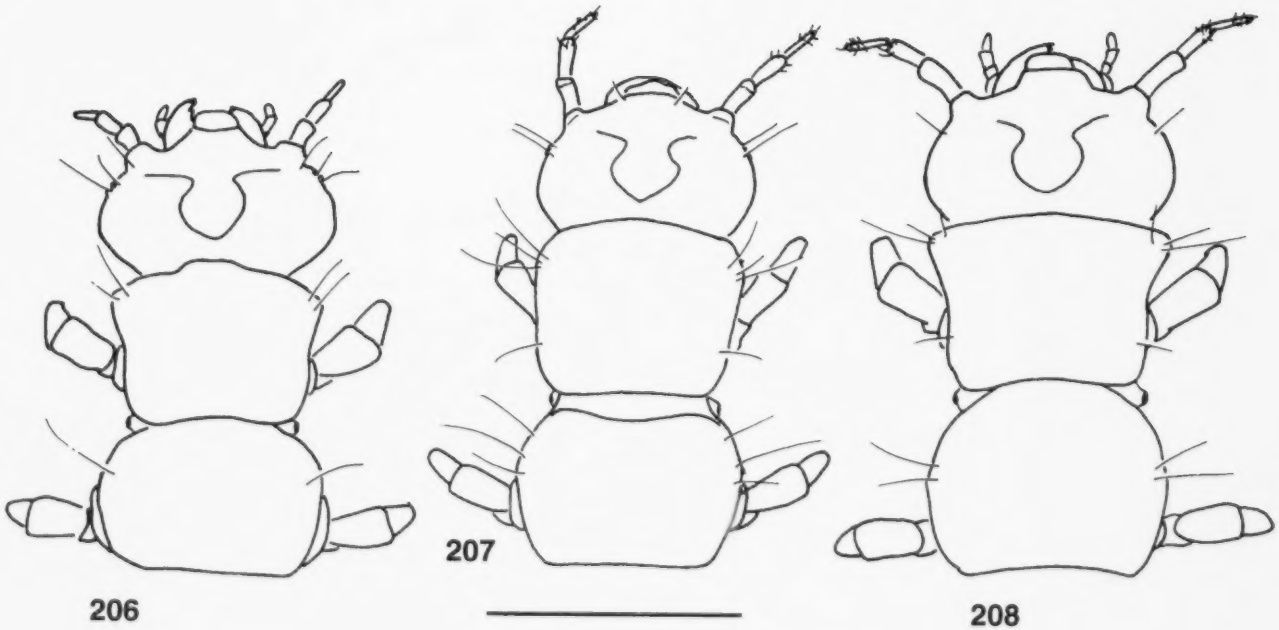


Plate 29 (larval forebodies 2).—**206**. Exocalopus sp. **207**. Cycloderus sp. **208**. Morpholycus costipennis Lea. [Scale bar = 2.0 mm (Figs. 207, 208); 1.6 mm (Fig. 206)]

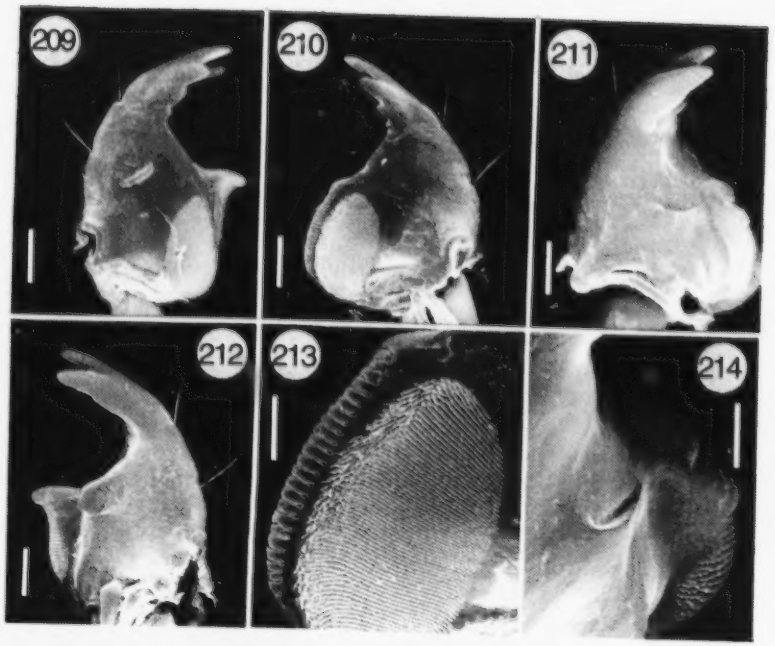


Plate 30 (larval mouthparts of Morpholycus costipennis Lea).—**209**. left mandible, dorsal. **210**. right mandible, dorsal. **211**. right mandible, ventral. **212**. left mandible, ventral. **213**. detail of right mandible, dorsal. **214**. detail of right mandible, ventral. [Scale bar = 0.2 mm (Figs. 209-212); 0.08 mm (Figs. 213-214)]

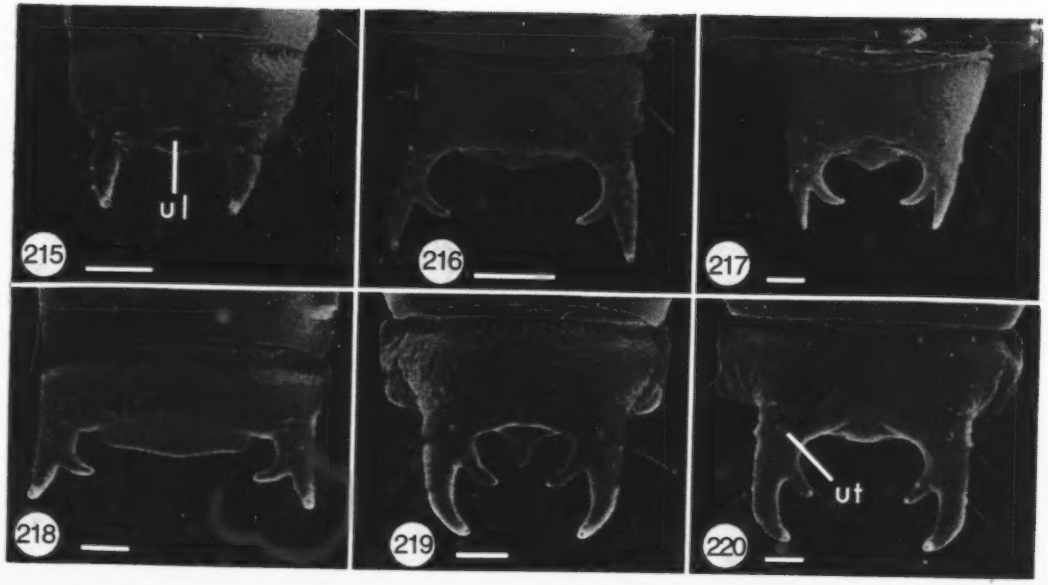


Plate 31 (urogomphal plate, dorsal).—**215**. Temnopalpus sp. larval type 1. **216**. Binburrum sp. **217**. Cycloderus sp. **218**. Morpholycus monilicornis Lea. **219**. M. costipennis Lea. **220**. M. apicalis (Macleay). ul = urogomphal lip; ut = urogomphal tubercle. [Scale bar = 0.4 mm]

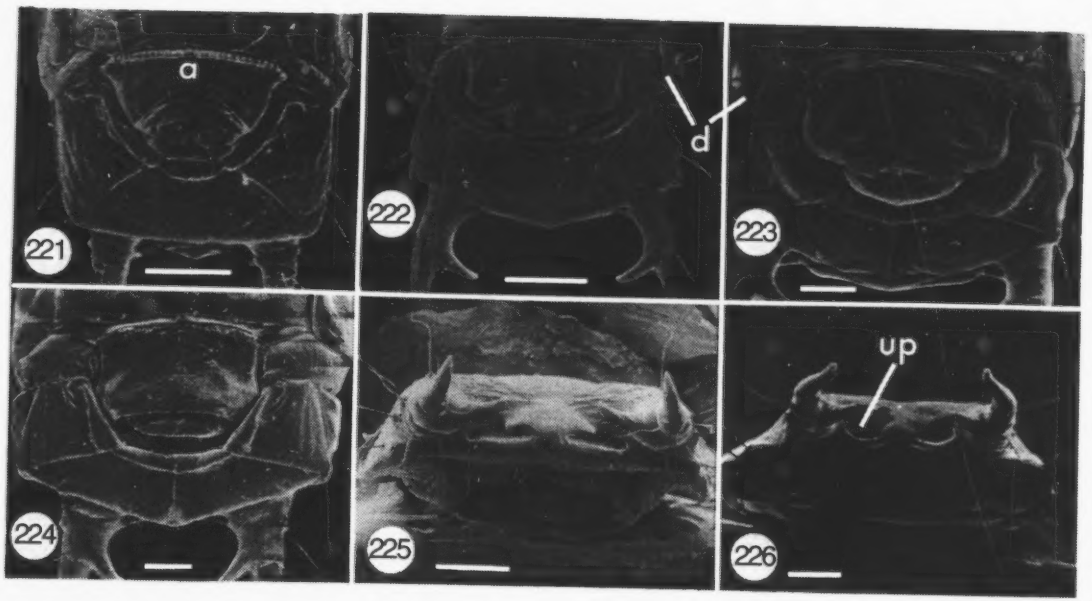


Plate 32 (urogomphal plate, ventral and caudal).—221-224. Ventral view.**221**. Temnopalpus sp. larval type 1. **222**. Binburrum sp. **223**. Morpholycus monilicornis Lea. **224**. M. apicalis (Macleay). 225-226. Caudal view. **225**. Cycloderus sp. **226**. Morpholycus apicalis. a = asperities; d = dentiform process; up = urogomphal pit. [Scale bar = 0.4 mm]

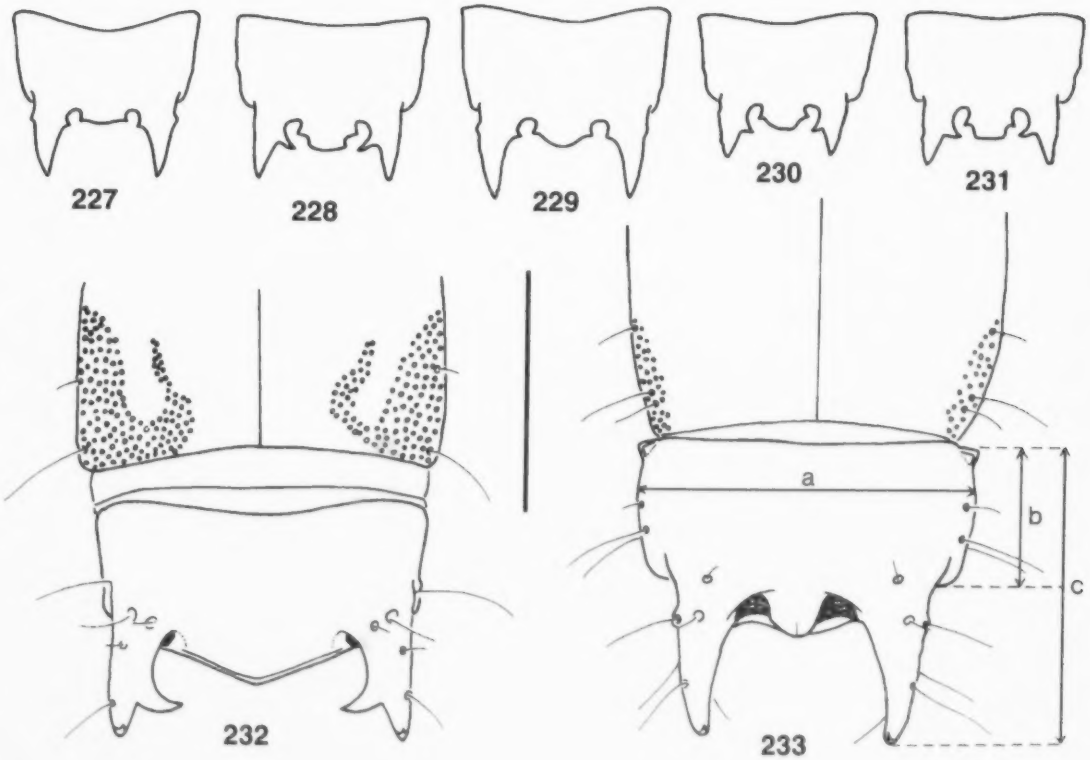


Plate 33 (urogomphal plate, dorsal).—227-231. Temnopalpus larval types. **227**. Type 1 (VIC, Cambarville). **228**. Type 2 (TAS, Lower Gordon River). **229**. Type 3 (TAS, Lake St. Clair). **230**. Type 4 (WA, nr. Nornalup). **231**. Type 5 (ACT, Wombat Creek). **232**. Techmessodes sp. **233**. Exocalopus sp. a = maximum urogomphal plate width; b= urogomphal plate length, excluding urogomphi; c = urogomphal plate length, including urogomphi [Scale bar = 1.0 mm]

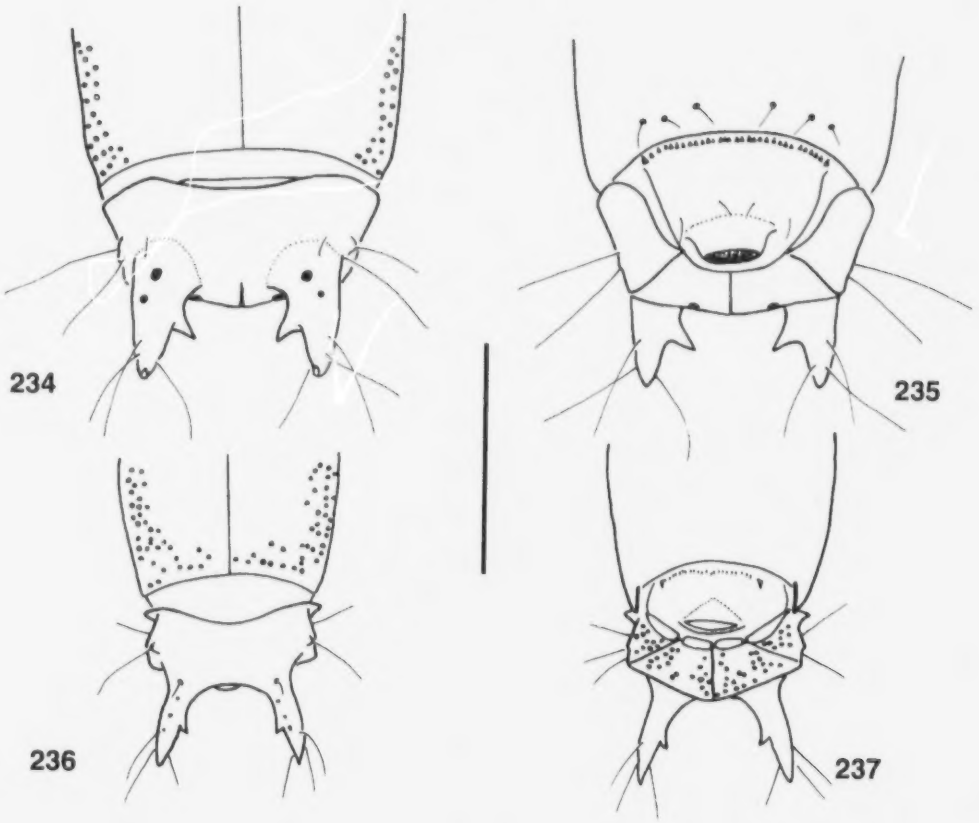


Plate 34 (urogomphal plate, dorsal and ventral).—**234**. Paromarteon sp., dorsal. **235**. ditto, ventral. **236**. Binburrum sp., dorsal. **237**. ditto, ventral. Both specimens from NSW, Wollomombi Falls, 40 km E. Armidale. [Scale bar = 1.0 mm]

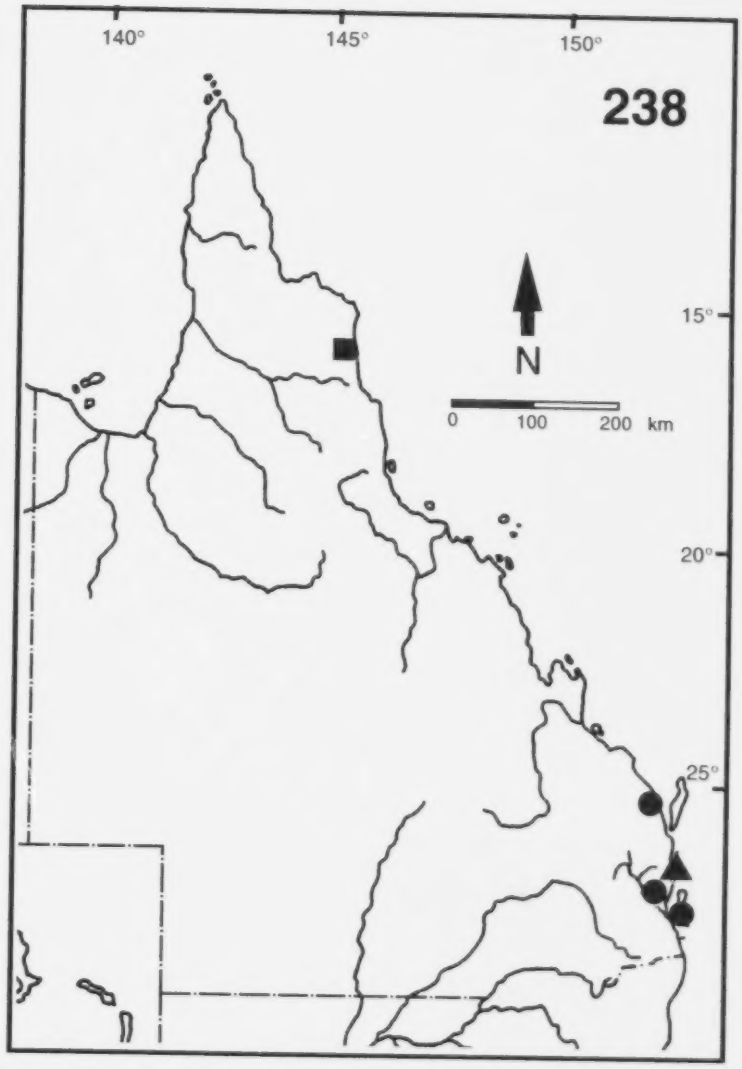


Figure 238. Known geographical distribution of Paromarteon constans Lea (squares); Paromarteon apicale Lea (circles and triangles); Paromarteon parvum Lea and Paromarteon fasciatum Lea (triangle).

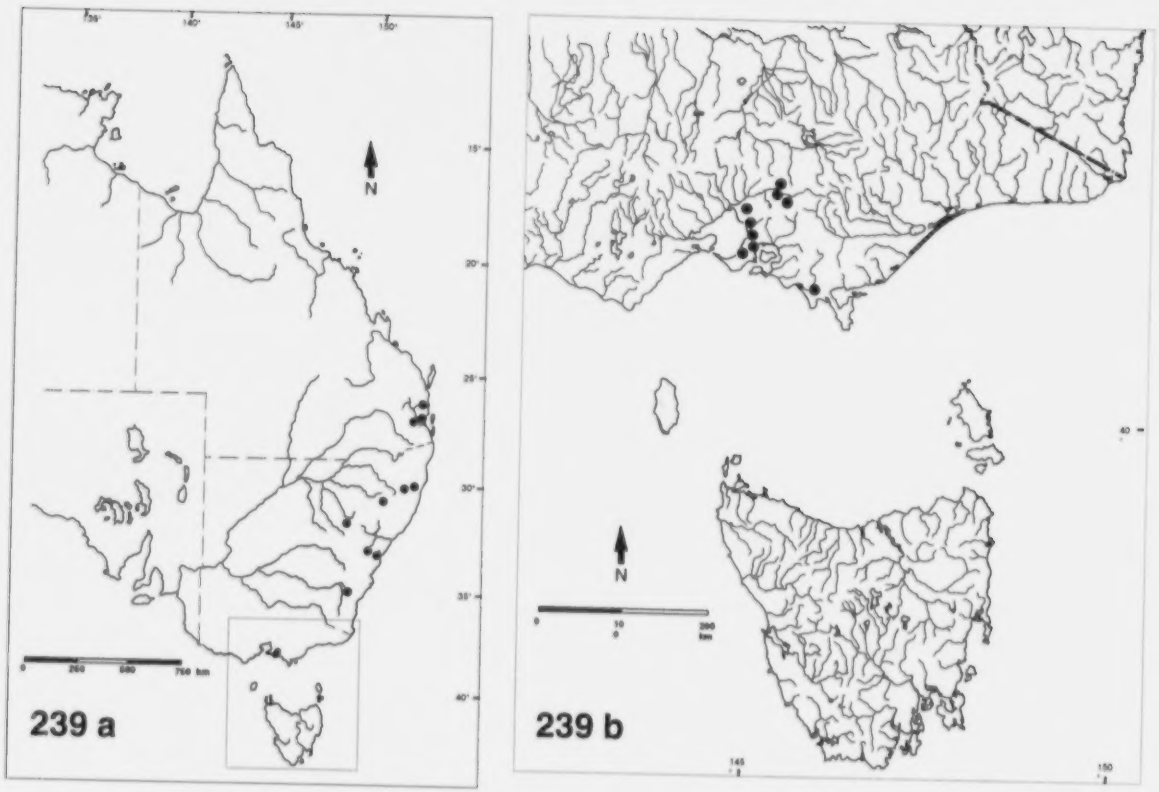


Figure 239. Known geographical distribution of Paromarteon mutabile Blackburn. **239a**. Entire range. **239b**. Detail of Melbourne area, Victoria.

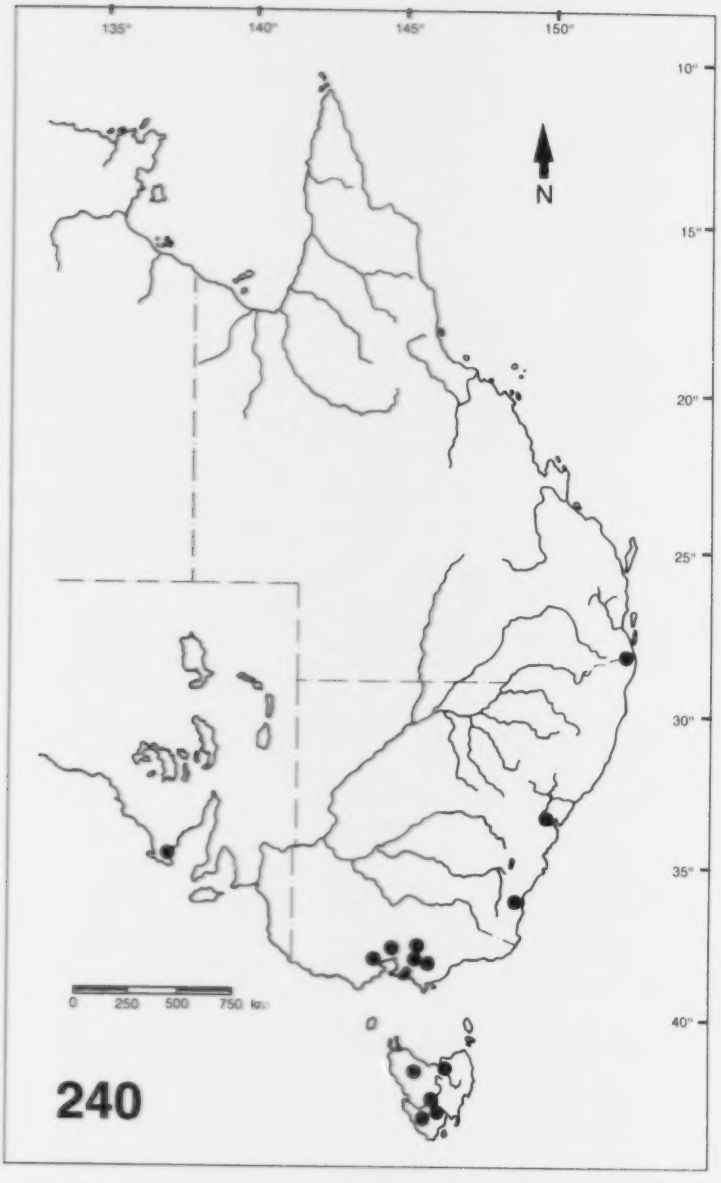


Figure 240. Known geographical distribution of Temnopalpus bicolor Blackburn.

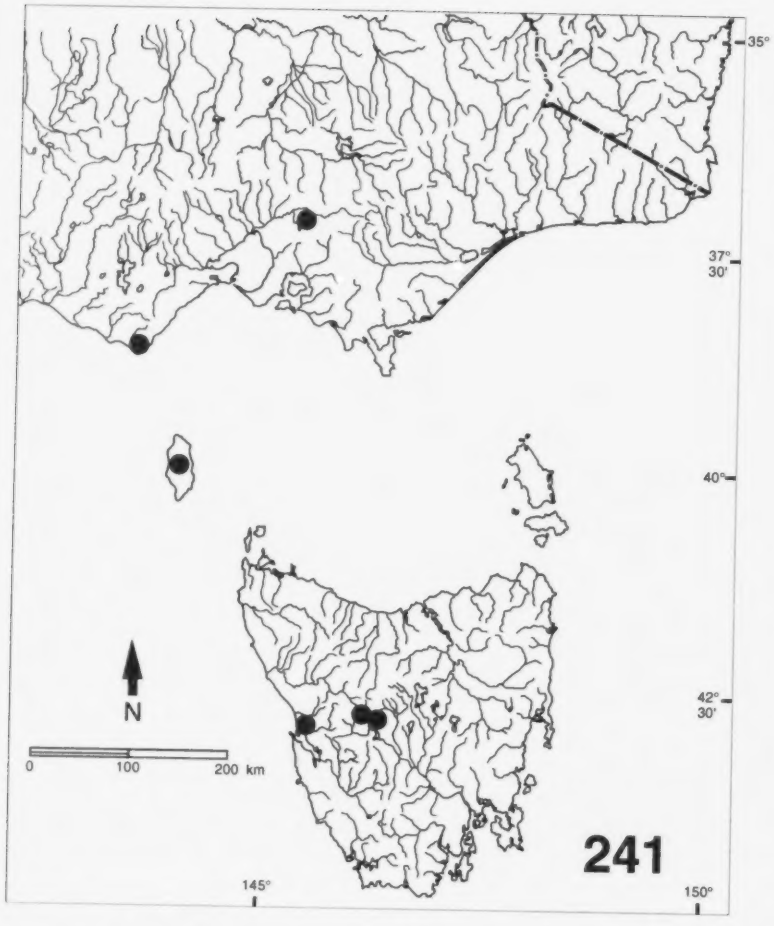


Figure 241. Known geographical distribution of Temnopalpus niger Lea.

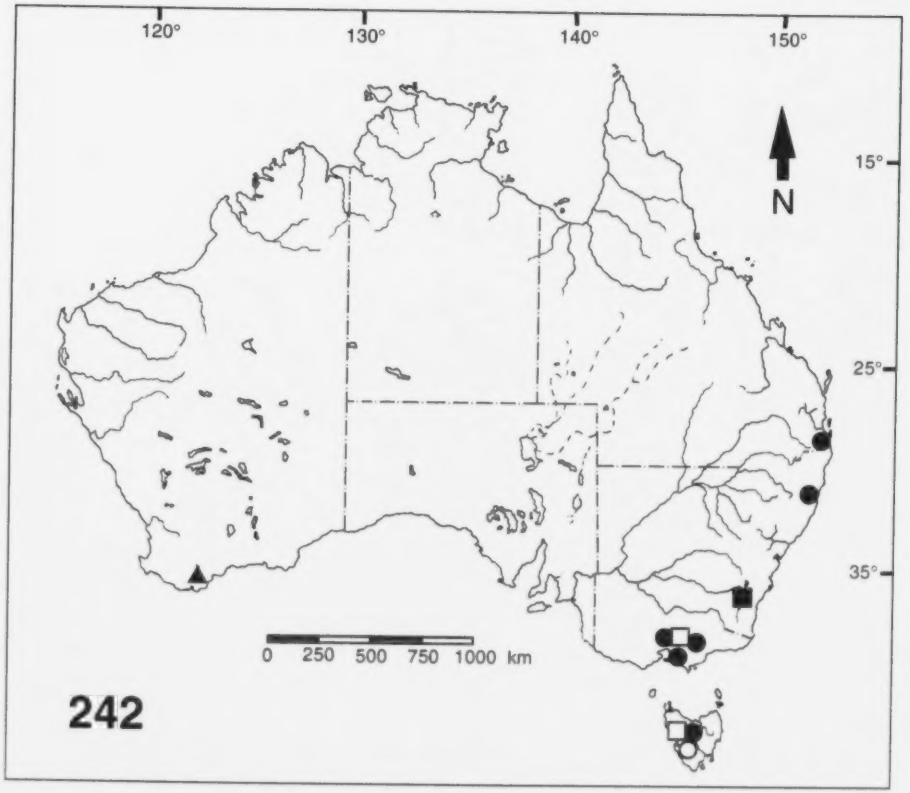


Figure 242. Geographical distribution of Temnopalpus larval types. Shaded circles - type 1; open circles - type 2; open squares - type 3; triangle - type 4; shaded square - type 5.

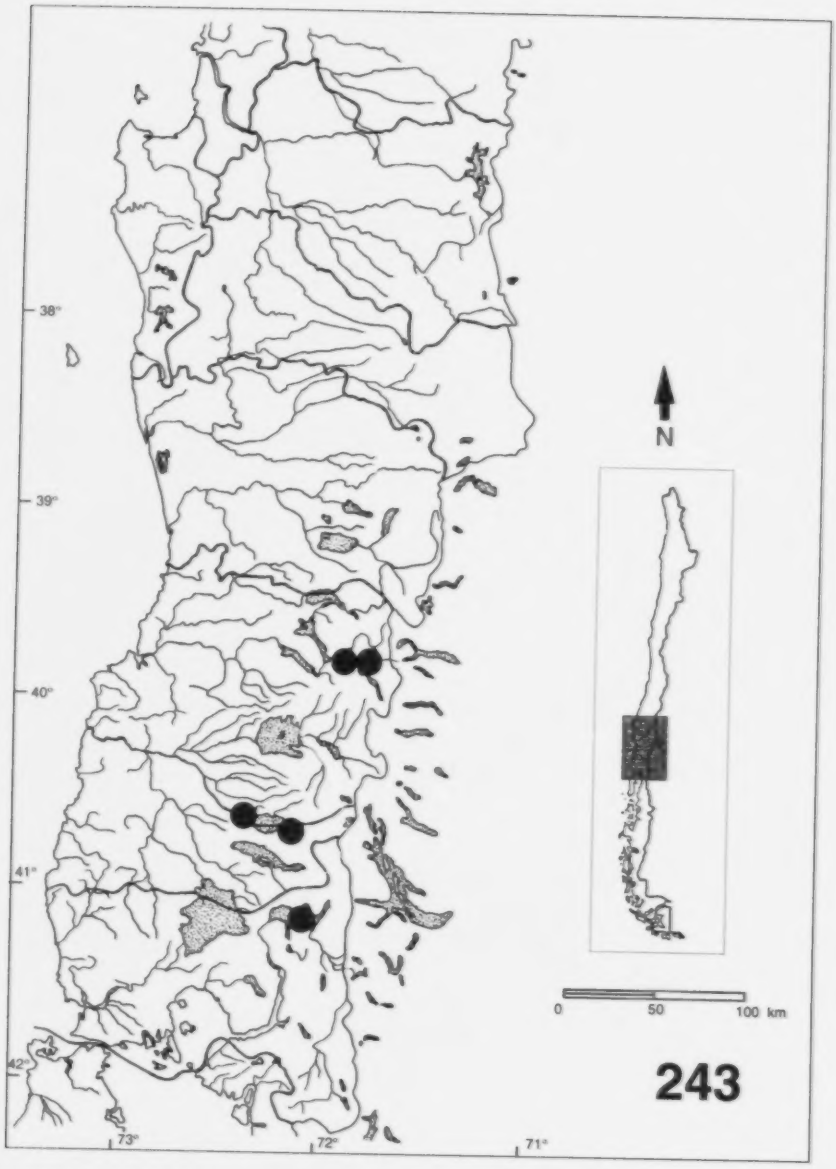


Figure 243. Known geographical distribution of Pilipalpus dasytoides Fairmaire.

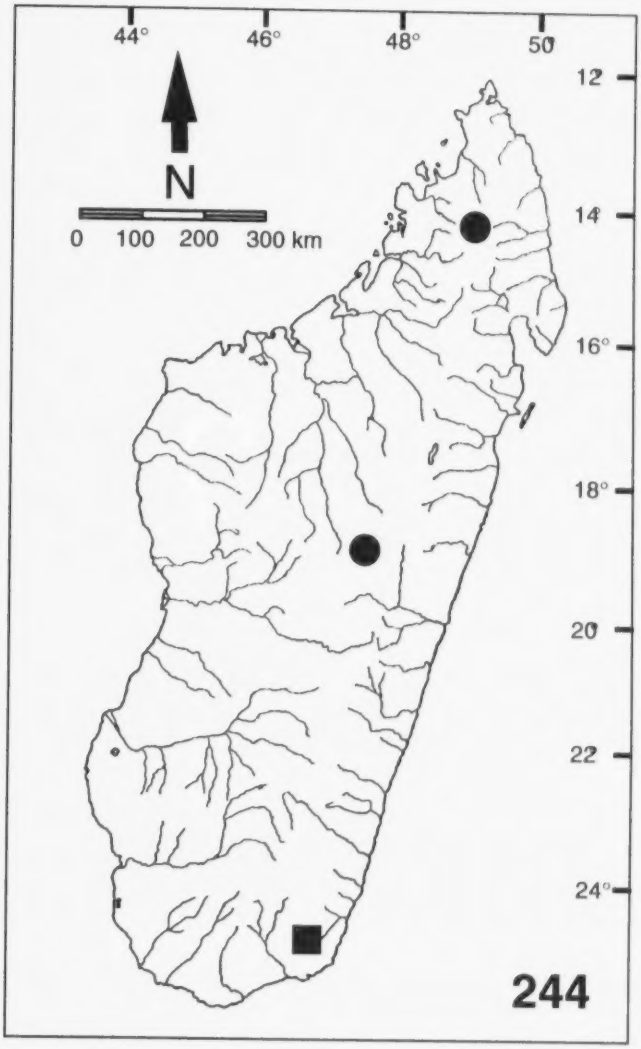
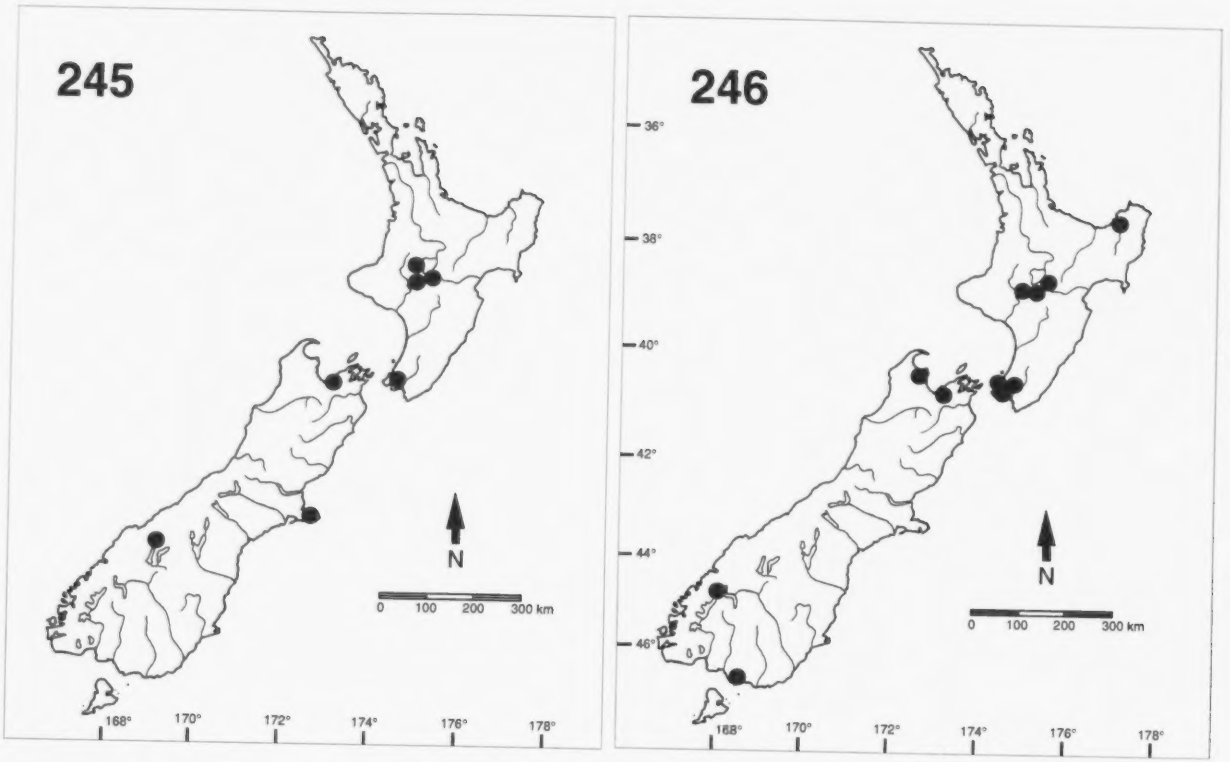
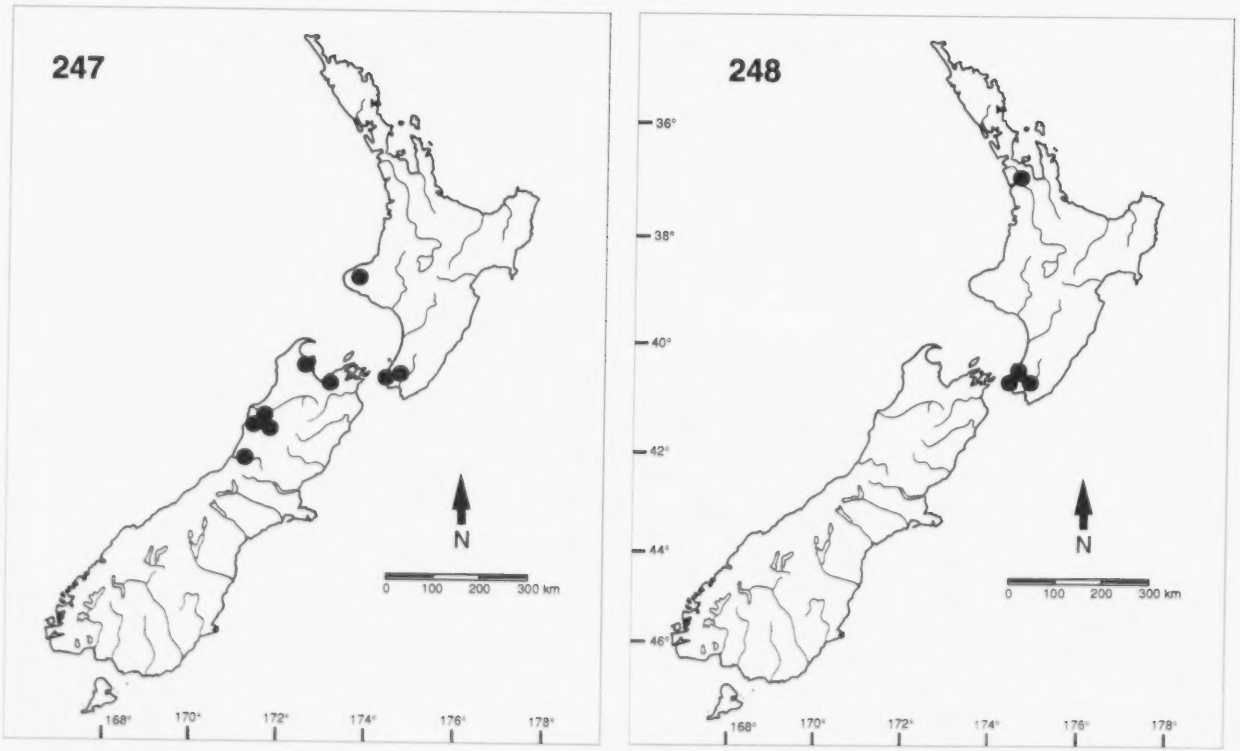


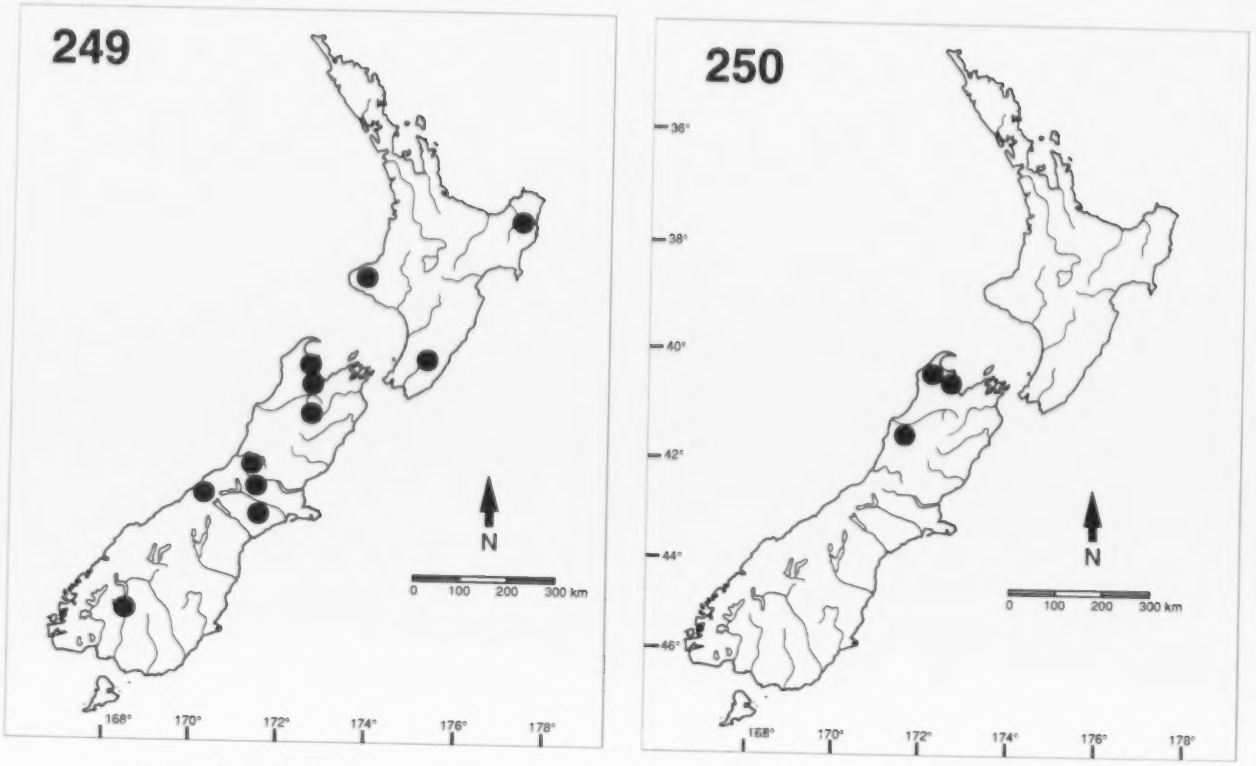
Fig. 244. Known geographical distribution of Incollogenius spp. (circles); Ranomafana steineri, gen. and sp. nov. (square); and Malagaethes lawrencei, gen. and sp. nov. (square).



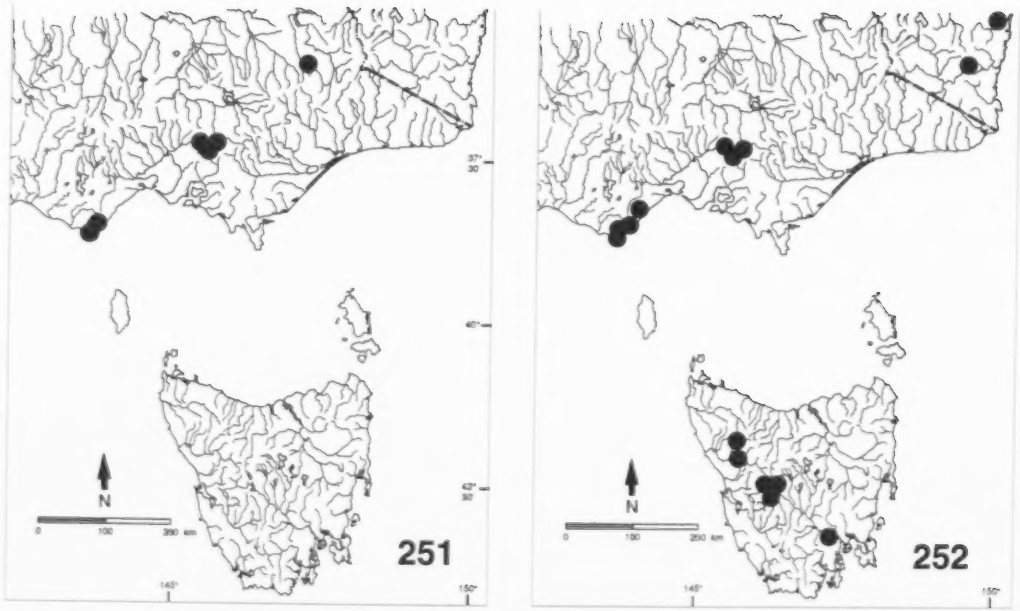
Figures 245-246. 245. Known geographical distribution of Techmessa concolor Bates. **246.** Known geographical distribution of Techmessa telephoroides Bates.



Figures 247-248. 247. Known geographical distribution of Techmessodes picticornis (Broun); **248.** Known geographical distribution of Techmessodes versicolor Broun.



Figures 249-250. 249. Known geographical distribution of Exocalopus spp. (adults); **250.** Geographical distribution of examined larvae of Exocalopus.



Figures 251-252. 251. Known geographical distribution of Binburrum concavifrons, sp. nov. **252.** Known geographical distribution of Binburrum ruficollis (Champion).

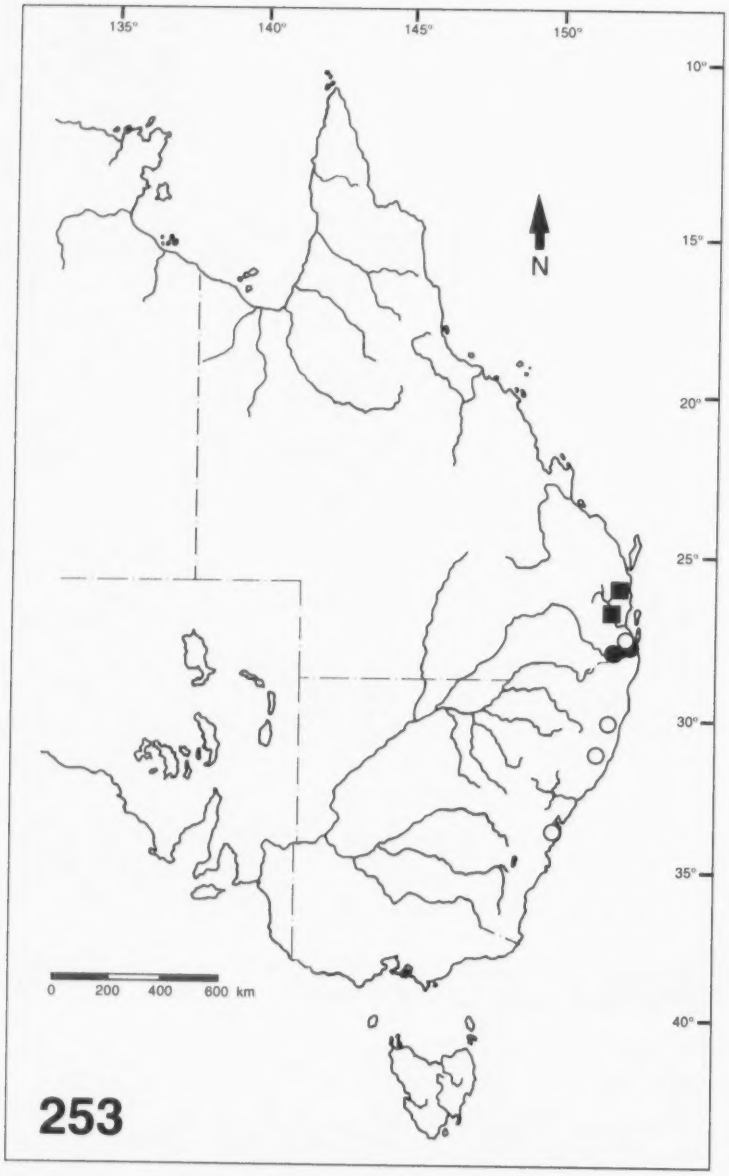


Figure 253. Known geographical distribution of Binburrum angusticollis, sp. nov. (shaded circles); Binburrum ephippiatum (Wiilson) (squares); and Binburrum bifoveicollis (Lea) (open circles)

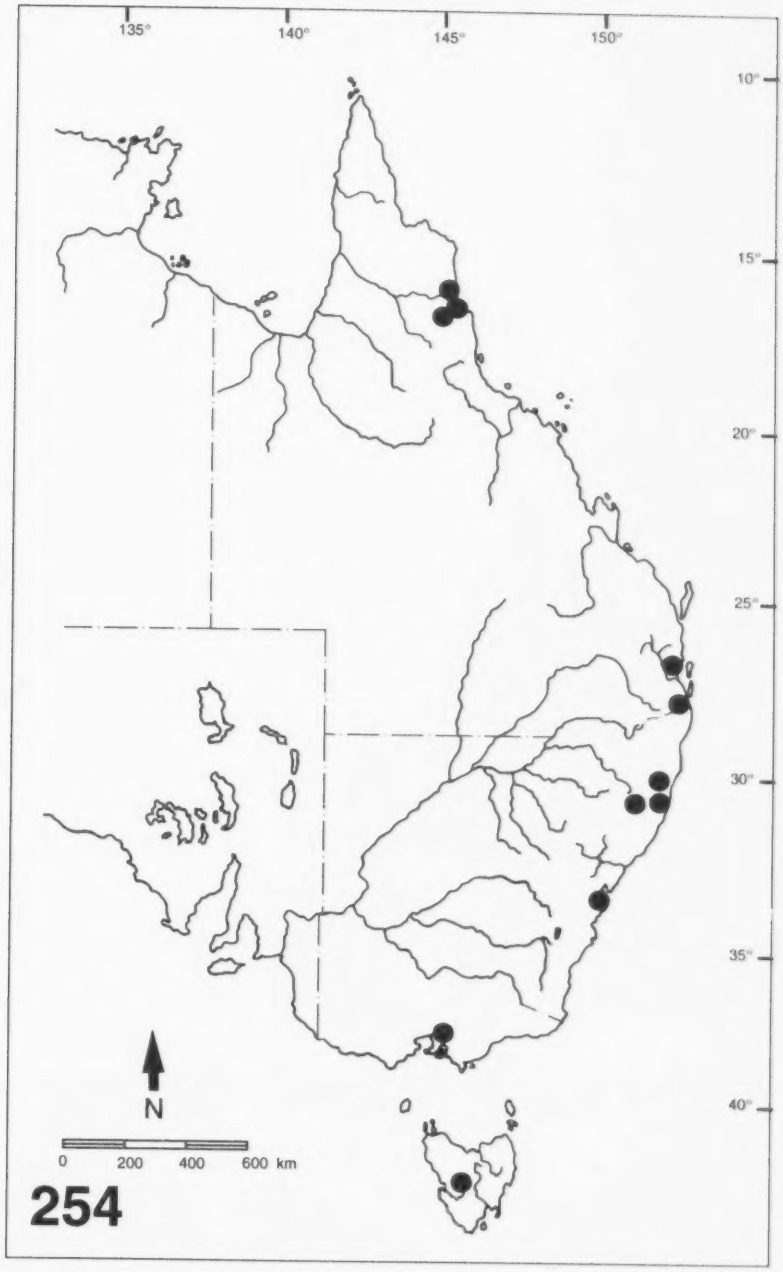
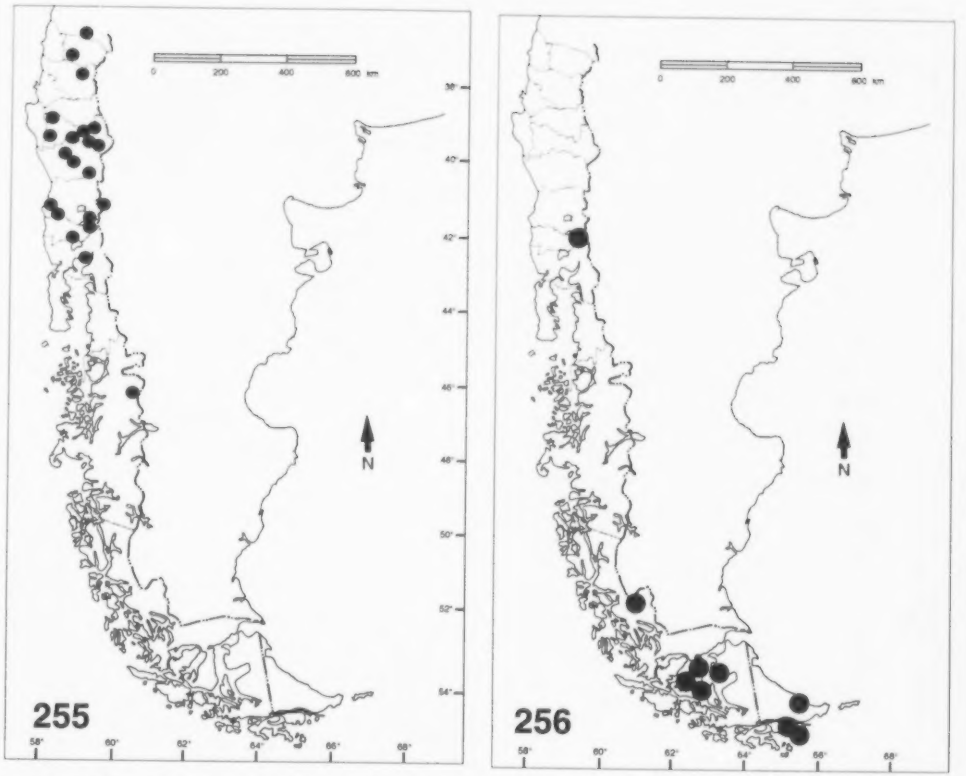
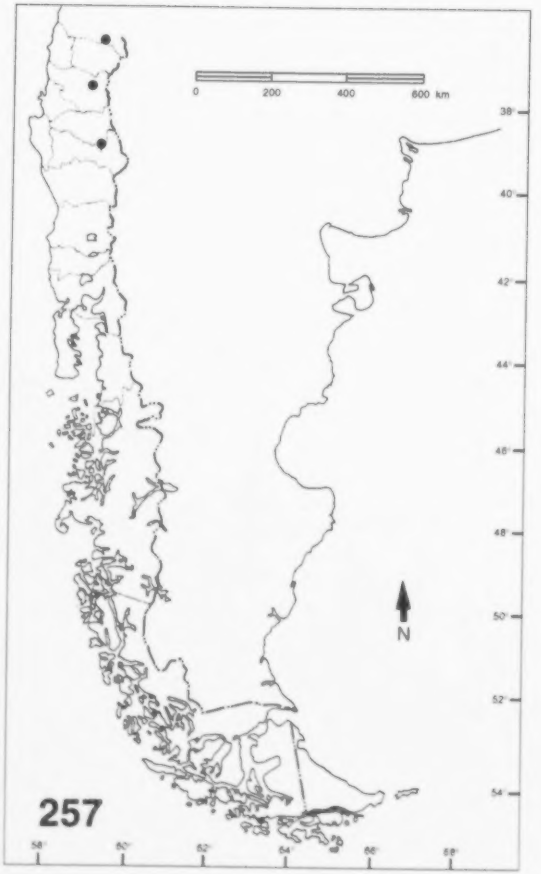
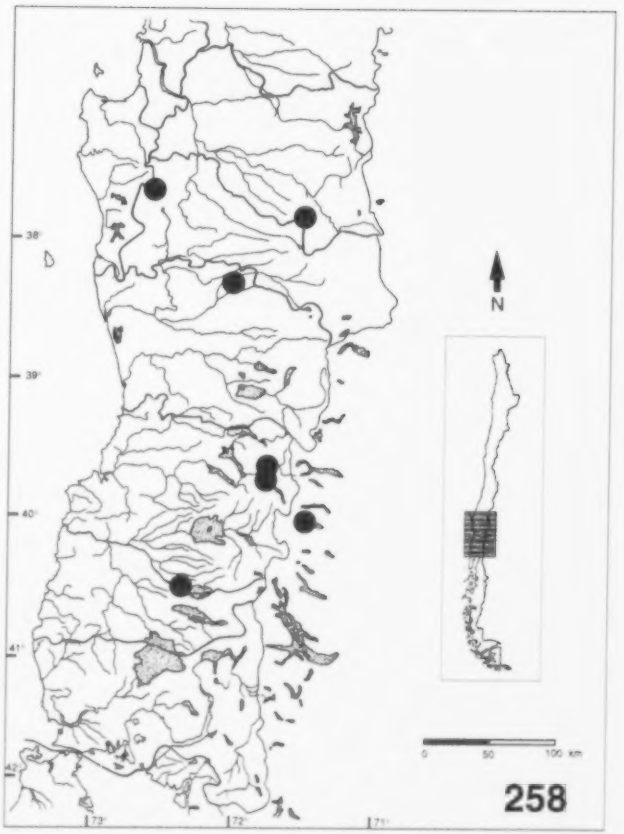


Figure 254. Geographical distribution of examined larvae of Binburrum spp.

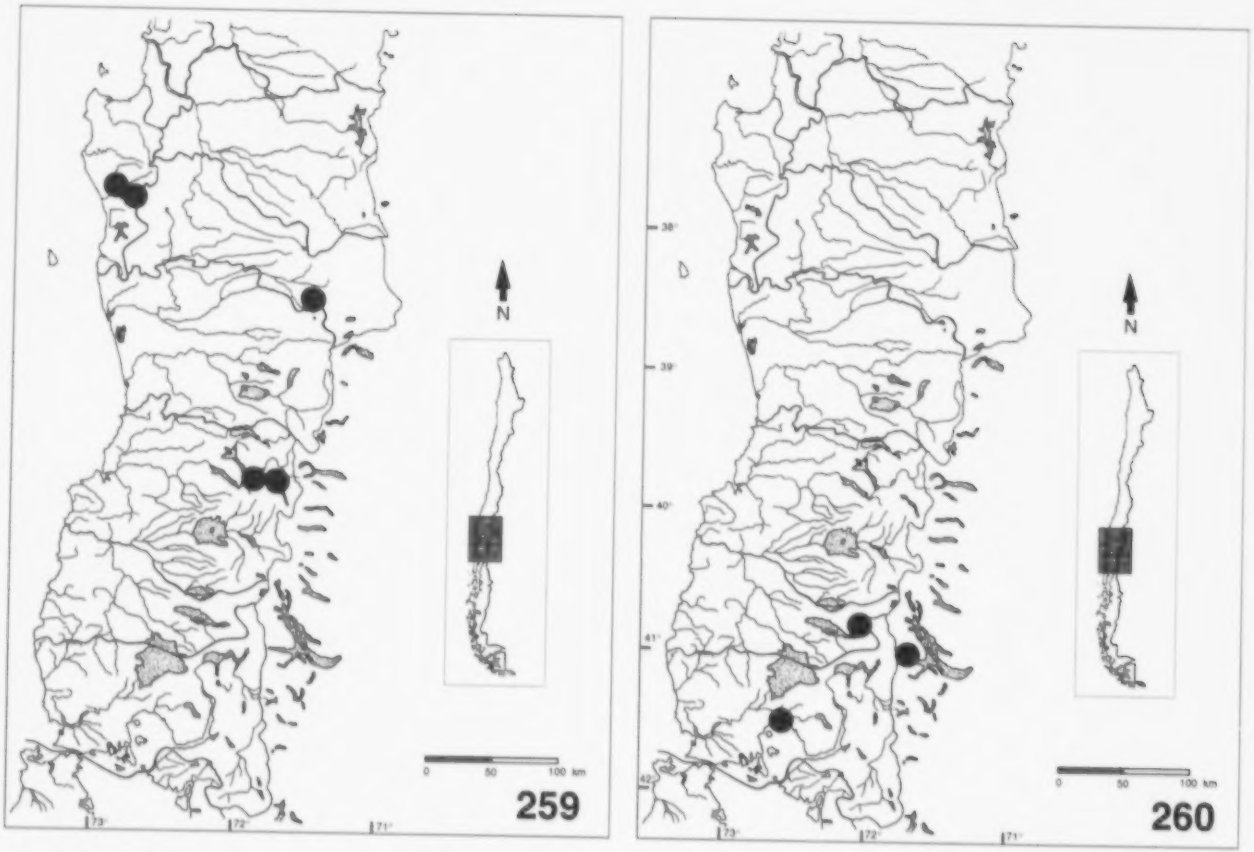


Figures 255-256. 255. Known geographical distribution of Cycloderus rubricollis Solier. **256**. Known geographical distribution of Cycloderus magellanicus Philippi.

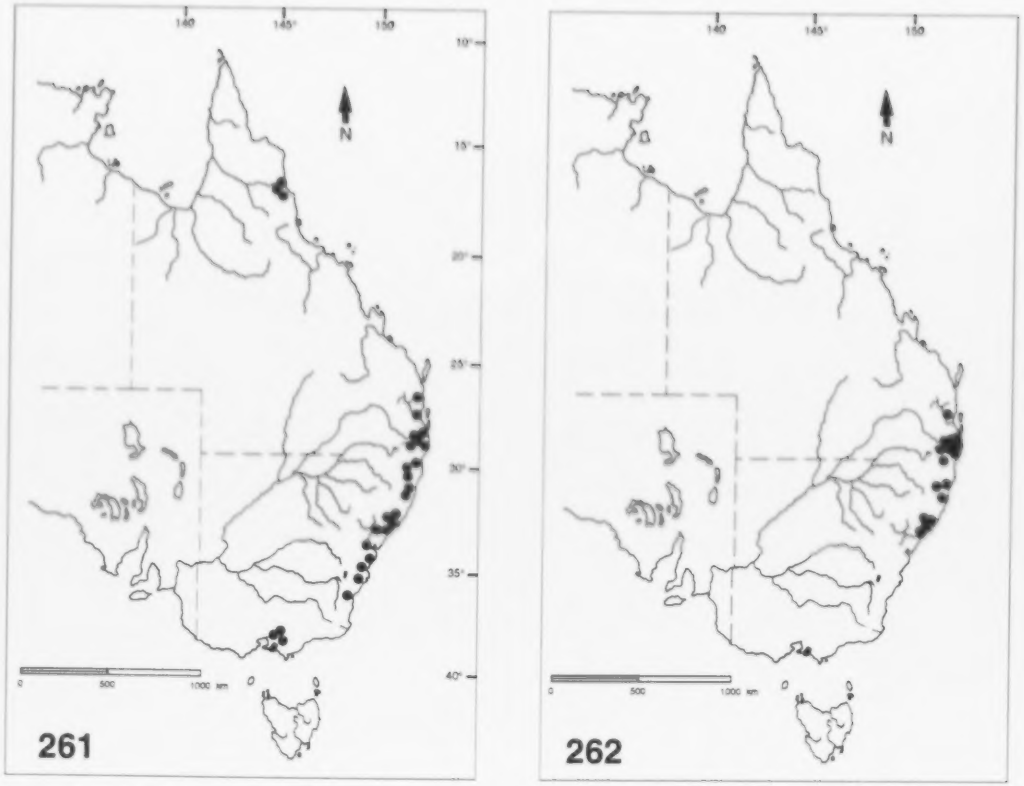




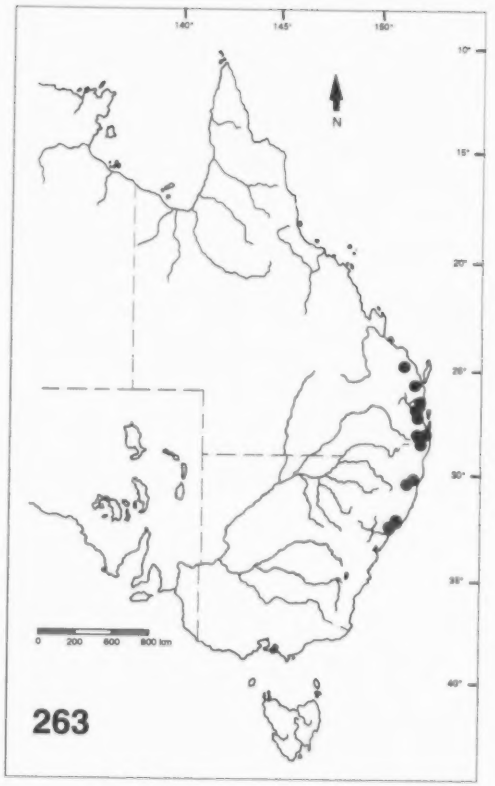
Figures 257-258. 257. Known geographical distribution of Cycloderus planipennis Fairmaire and Germain. **258**. Known geographical distribution of Cycloderus signaticollis Fairmaire and Germain.

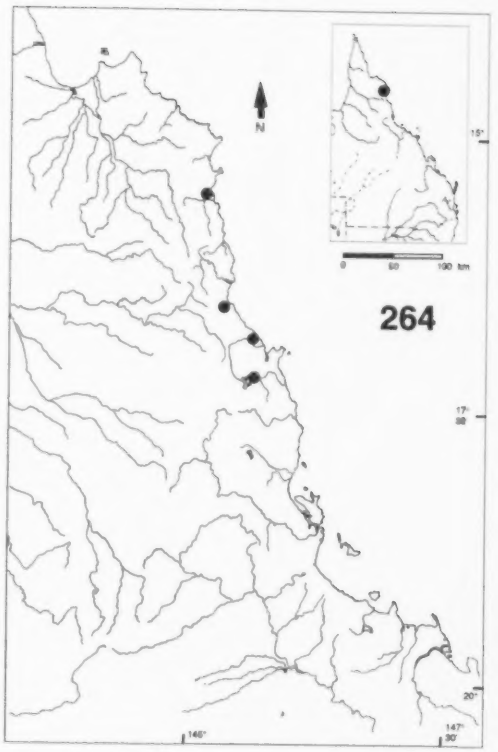


Figs. 259-260. **259**. Known geographical distribution of Cycloderus hirsutus, sp. nov. **260**. Known geographical distribution of Cycloderus immaculicollis, sp. nov.

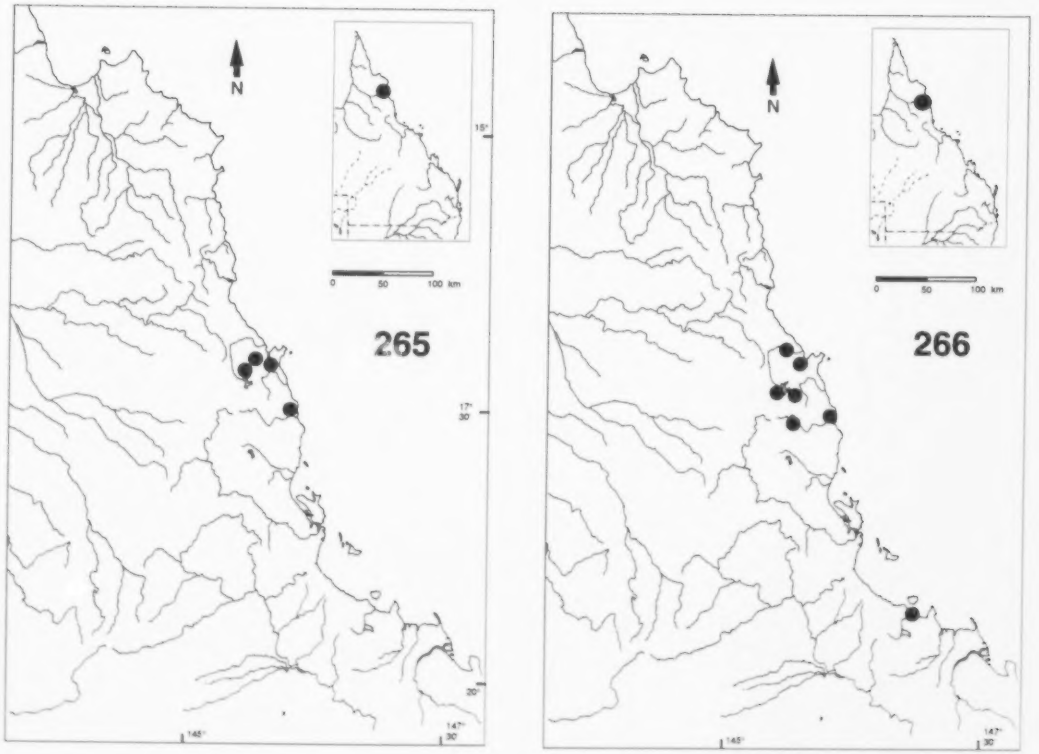


Figures 261-262. 261. Known geographical distribution of Morpholycus monilicornis Lea; **262**. Known geographical distribution of Morpholycus costipennis Lea

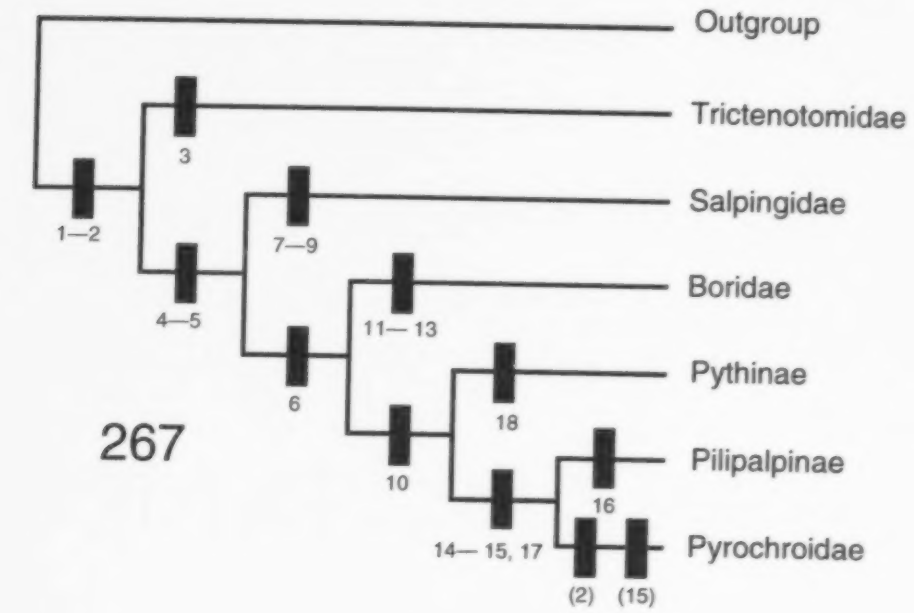


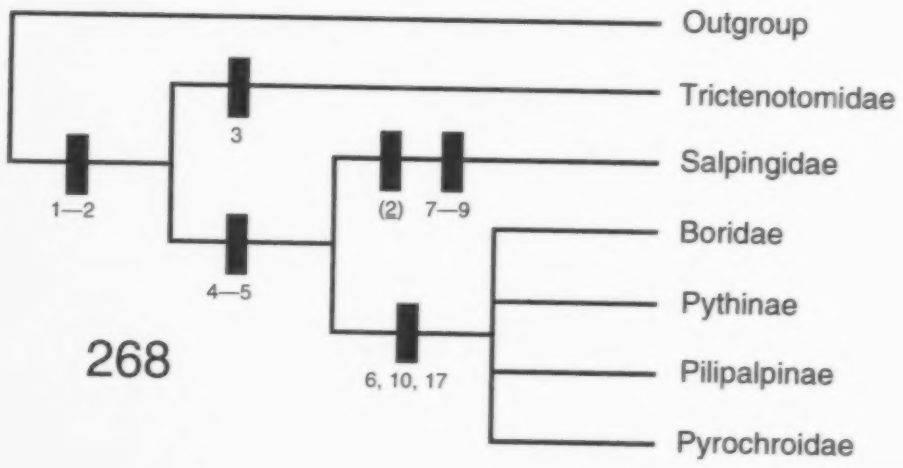


Figures 263-264. 263. Known geographical distribution of Morpholycus apicalis (Macleay); **264**. Known geographical distribution of Morpholycus nigripennis (Macleay)



Figures 265-266. 265. Known geographical distribution of Morpholycus concolor (Macleay); **266**. Known geographical distribution of Morpholycus flabellicornis (Macleay).





Figures 267-268. **267**. Strict consensus cladogram depicting the relationships among Trictenotomidae, Salpingidae, Boridae, Pythidae, and Pyrochroidae, according to Watt (1987); character matrix given in Table 1. **268**. Strict consensus cladogram depicting the relationships among Trictenotomidae, Salpingidae, Boridae, Pythidae, and Pyrochroidae, according to different interpretations of characters presented by Watt (1987); character matrix given in Table 2.

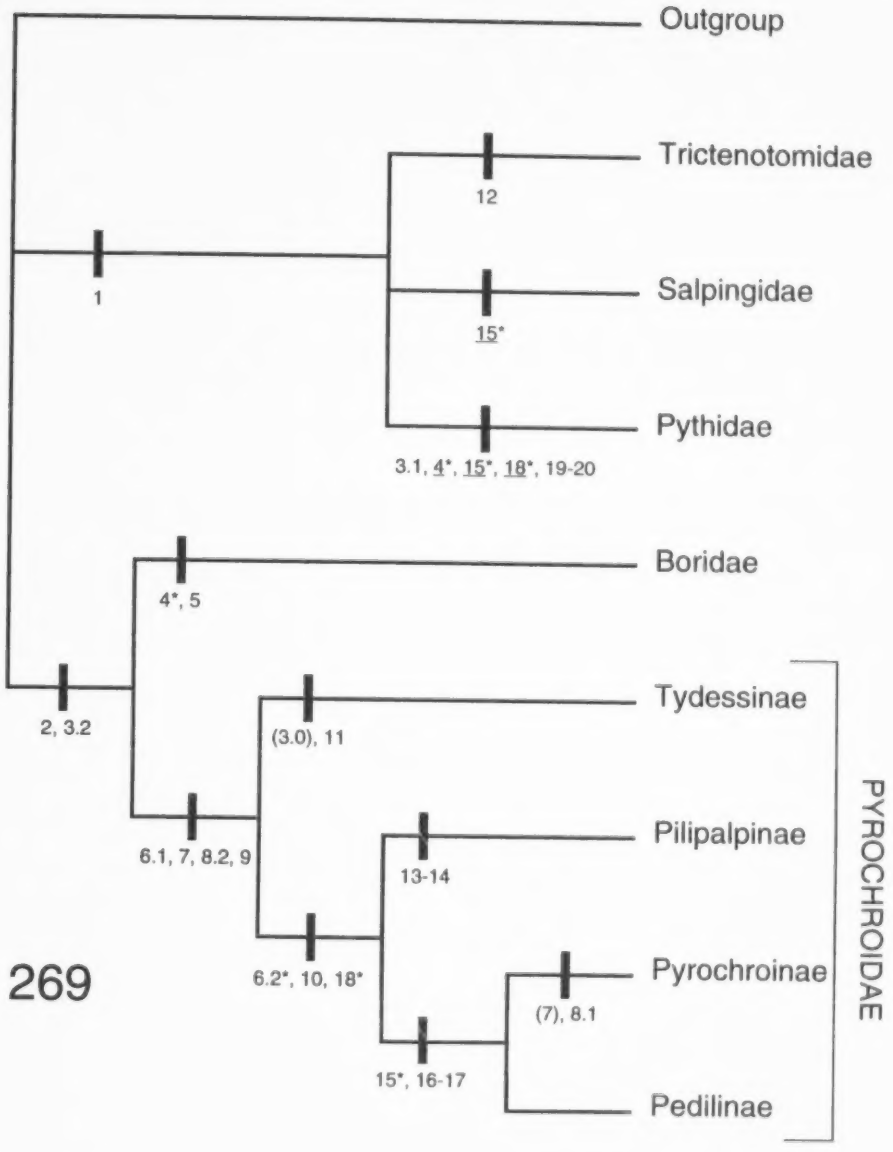


Figure 269. Strict consensus cladogram depicting relationships among Trictenotomidae, Salpingidae, Pythidae, Boridae, Tydessinae (genus Tydessa), Pilipalpinae, Pyrochroinae, and Pedilinae. Numerals with asterisks indicate homoplasy. Numerals with asterisks and underscoring indicate homoplasy in only some member(s) of the given taxon. Numerals in parentheses indicate reversals. Characters are given in the text, and the character matrix is given in Table 3.

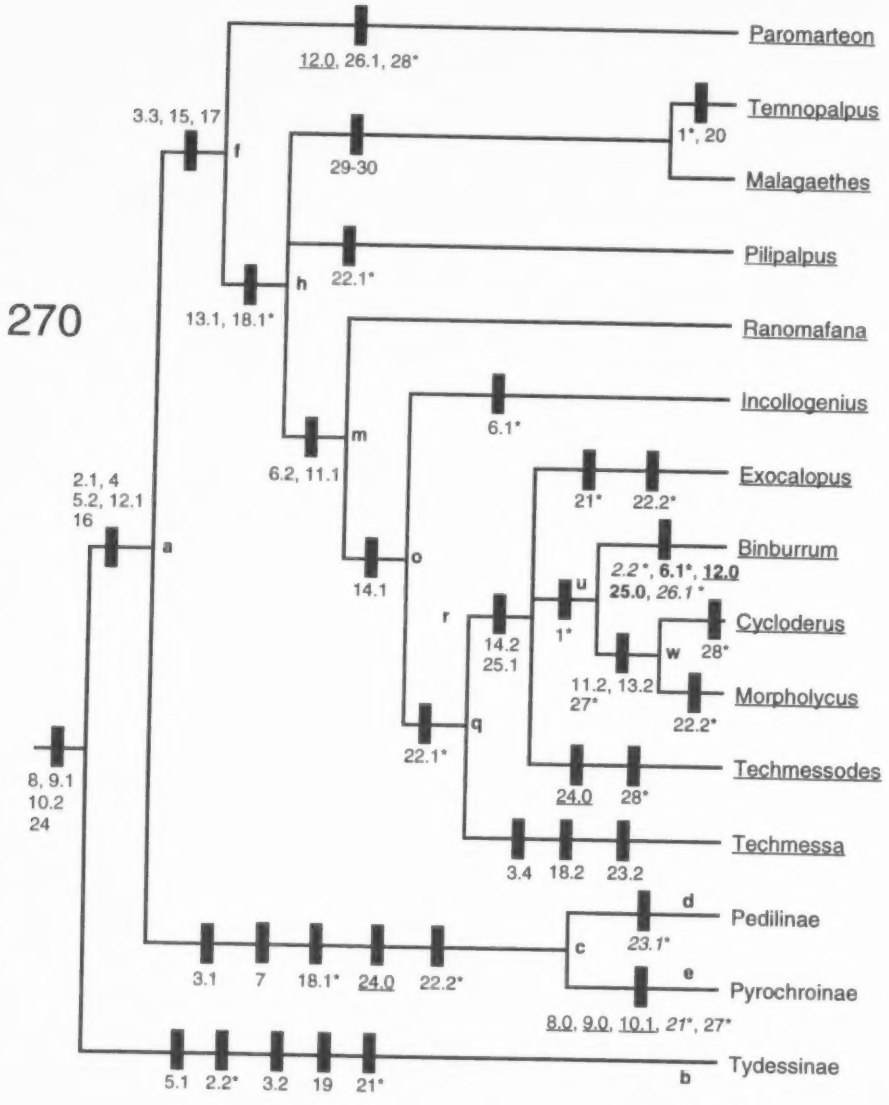


Figure 270. Cladogram depicting the phylogenetic relationships among Tydessinae, Pilipalpinae (individual genera), Pedilinae, and Pyrochroinae. Numerals with asterisks indicate homoplasy; numerals with underscoring indicate reversal; numerals in bold indicate reversal in some taxa only; numerals with outline and asterisk indicate homoplasy in some taxa only. Characters are given in the text; character matrix is given in Table 4.

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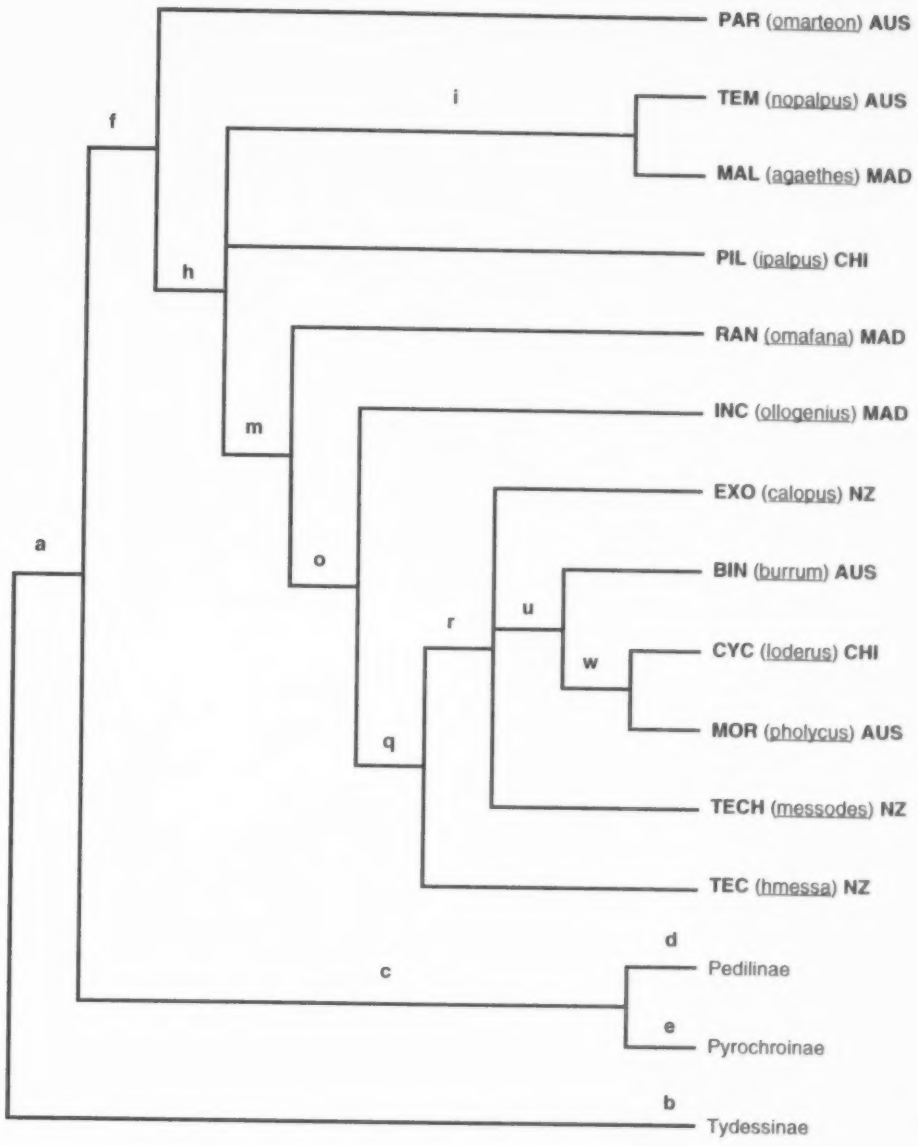


Figure 271. Cladogram (identical topology to Fig. 270) with labelled ancestral nodes for Brooks Parsimony Analysis (see Table 5 and Fig. 272).

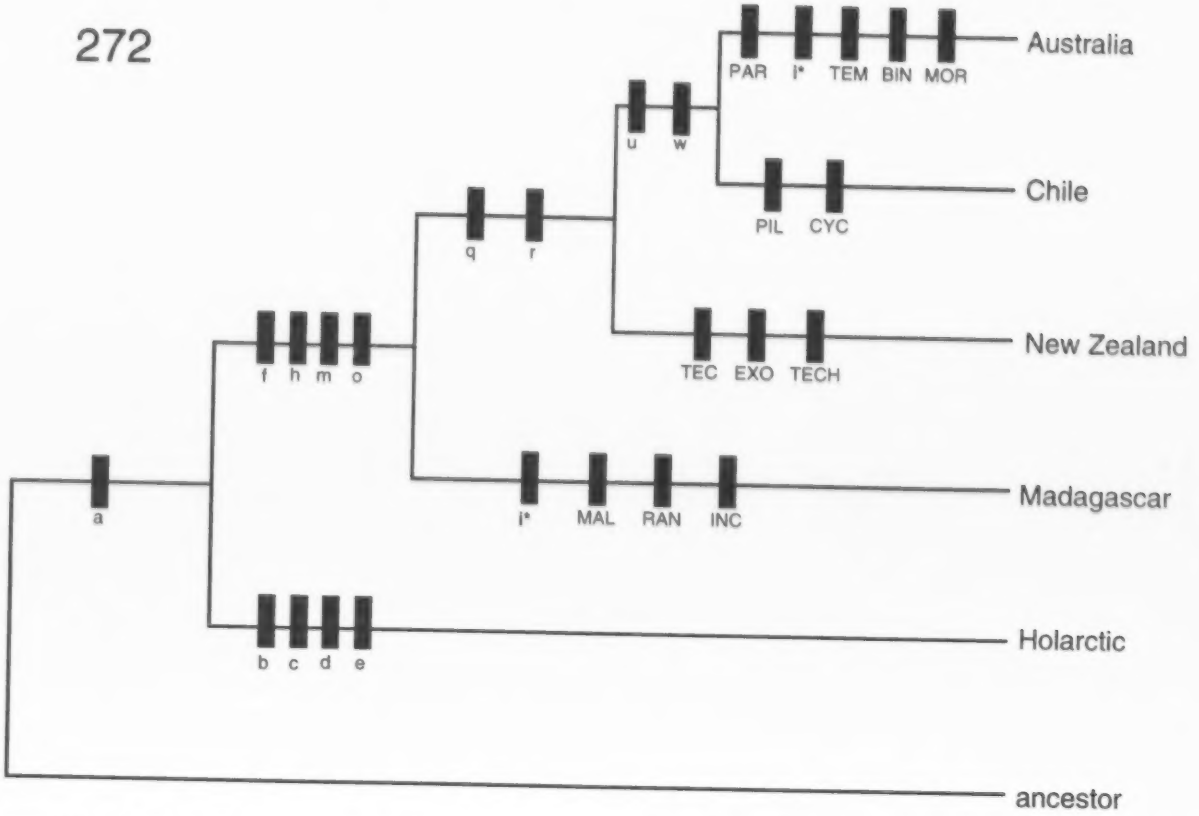


Figure 272. Area cladogram depicting the relationships among Holarctica, Madagascar, New Zealand, Chile, and Australia based on data from Pilipalpinae. A hypothetical ancestor was used to root the tree. Characters are given in Table 5. The asterisk indicates homoplasy in character i.

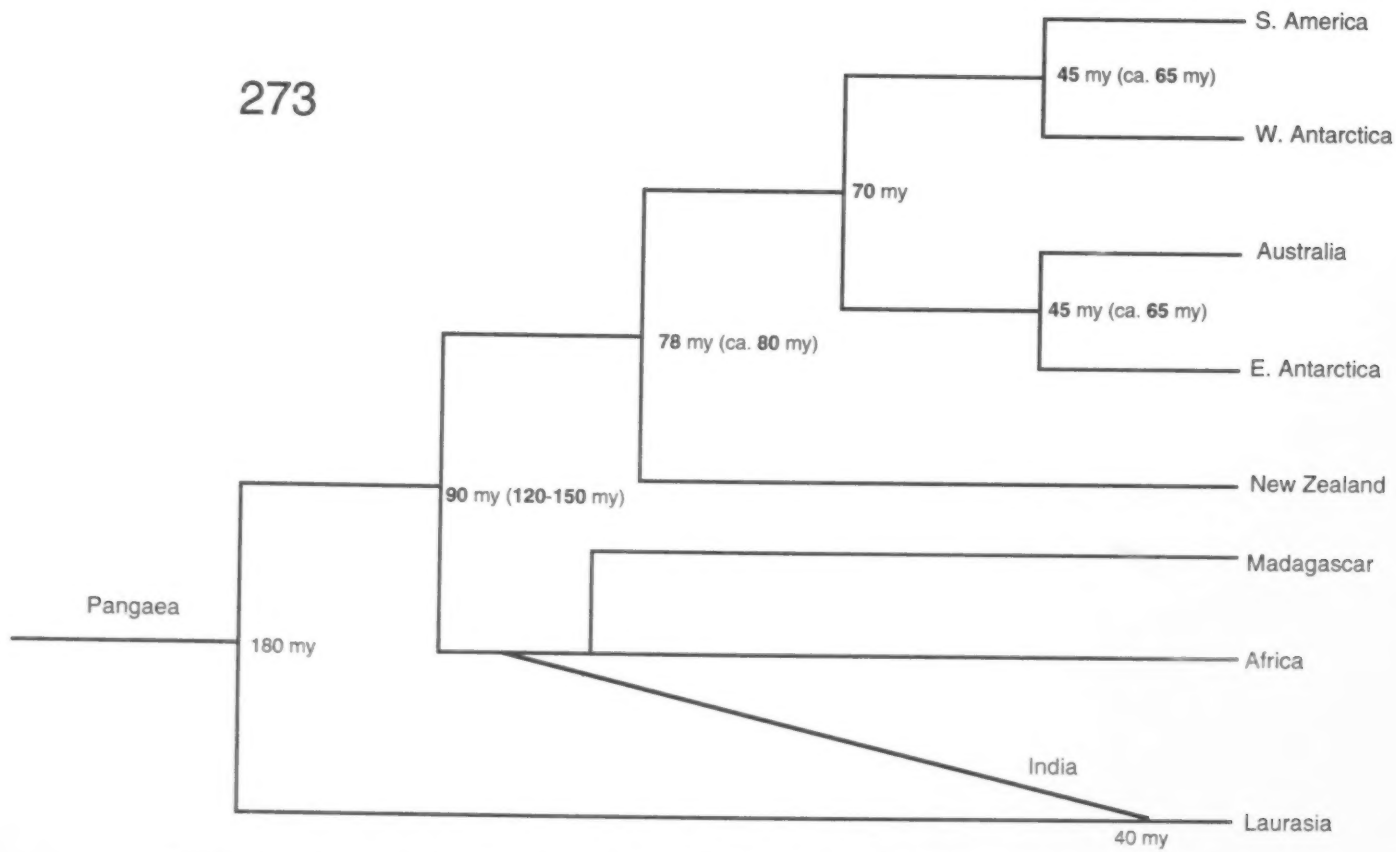
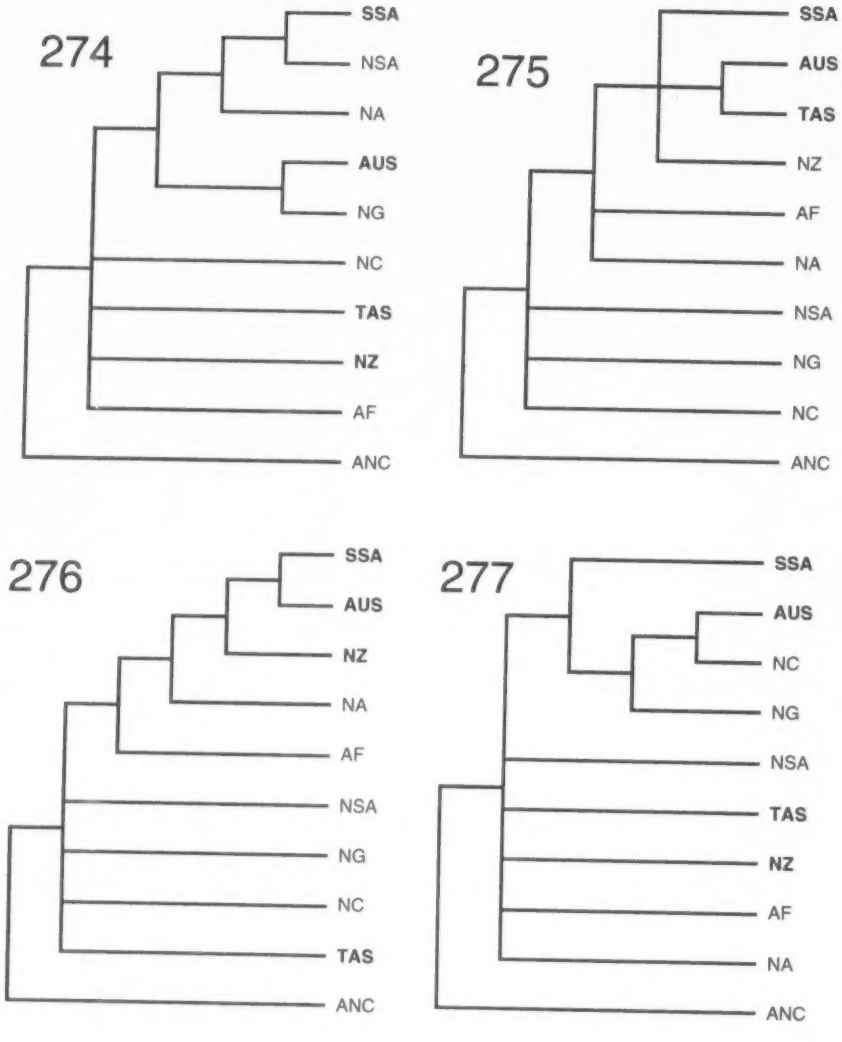
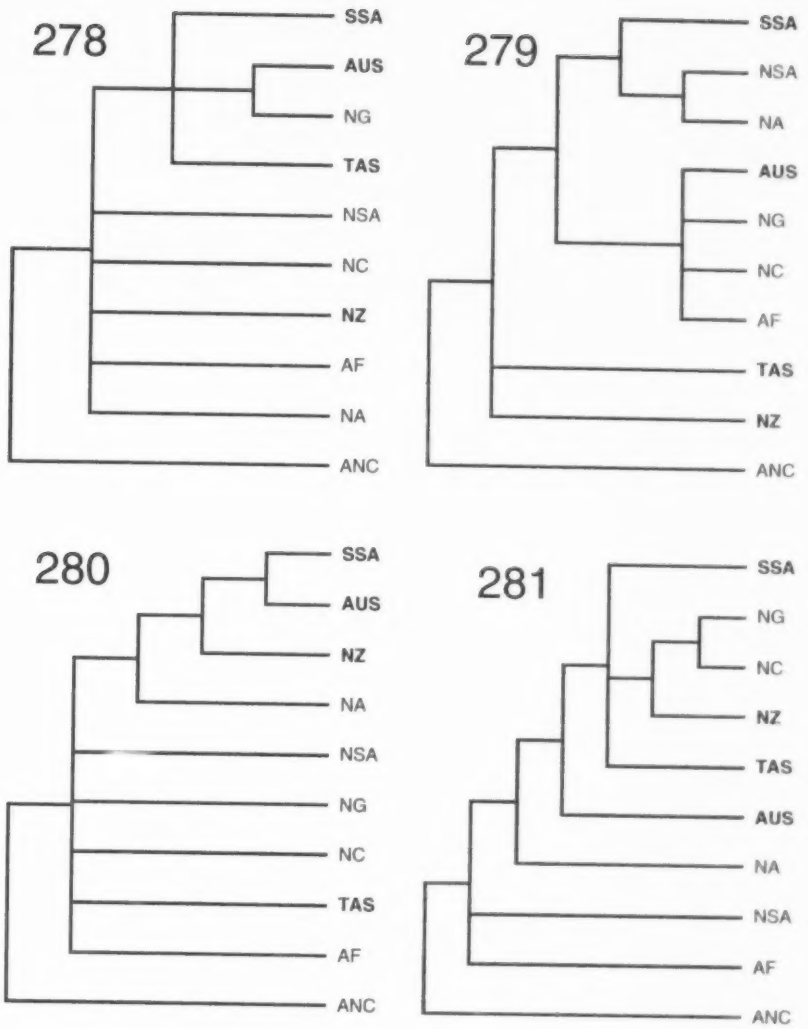


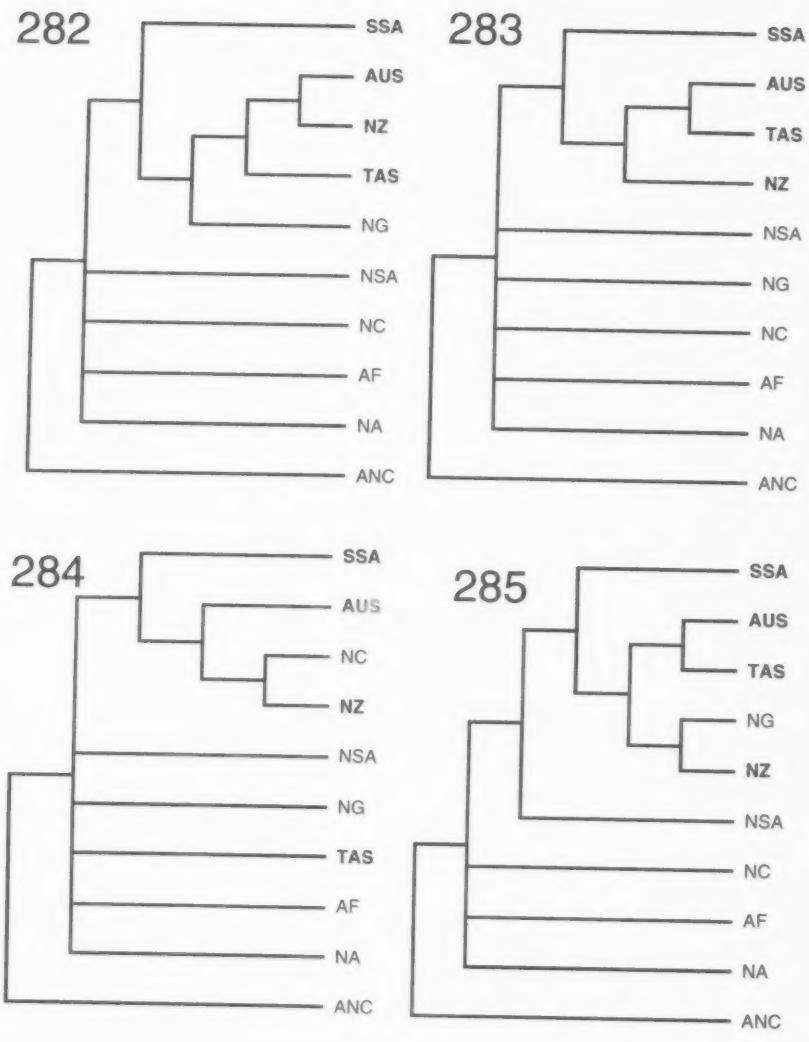
Figure 273. Area cladogram depicting the hypothetical break-up of Pangaea into Laurasia and Gondwanaland. Dates of separation are taken from Rosen (1978); dates in parentheses are taken from Thayer (1985).



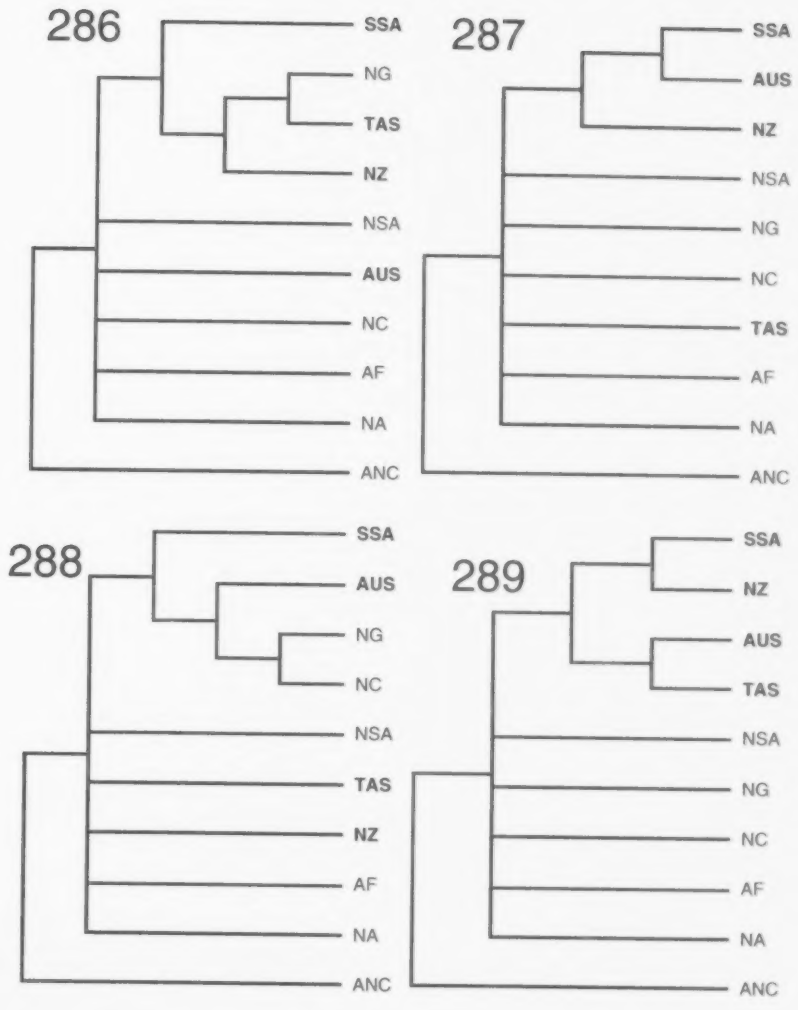
Figures 274-277. Area cladograms depicting the relationships among southern South America (SSA), northern South America (NSA), Australia (AUS), New Guinea (NG), New Caledonia (NC), Tasmania (TAS), New Zealand (NZ), South Africa (AF), and North America. Areas indicated in bold print are areas inhabited also by Pilipalpinae. **274**. Oxelytrum - Ptomaphila (Coleoptera: Silphidae). **275**. Diamesinae (Diptera: Chironomidae). **276**. Podonominae (Diptera: Chironomidae). **277**. Crinodendron - Dubouzetia - Peripentadenia (Elaeocarpaceae).



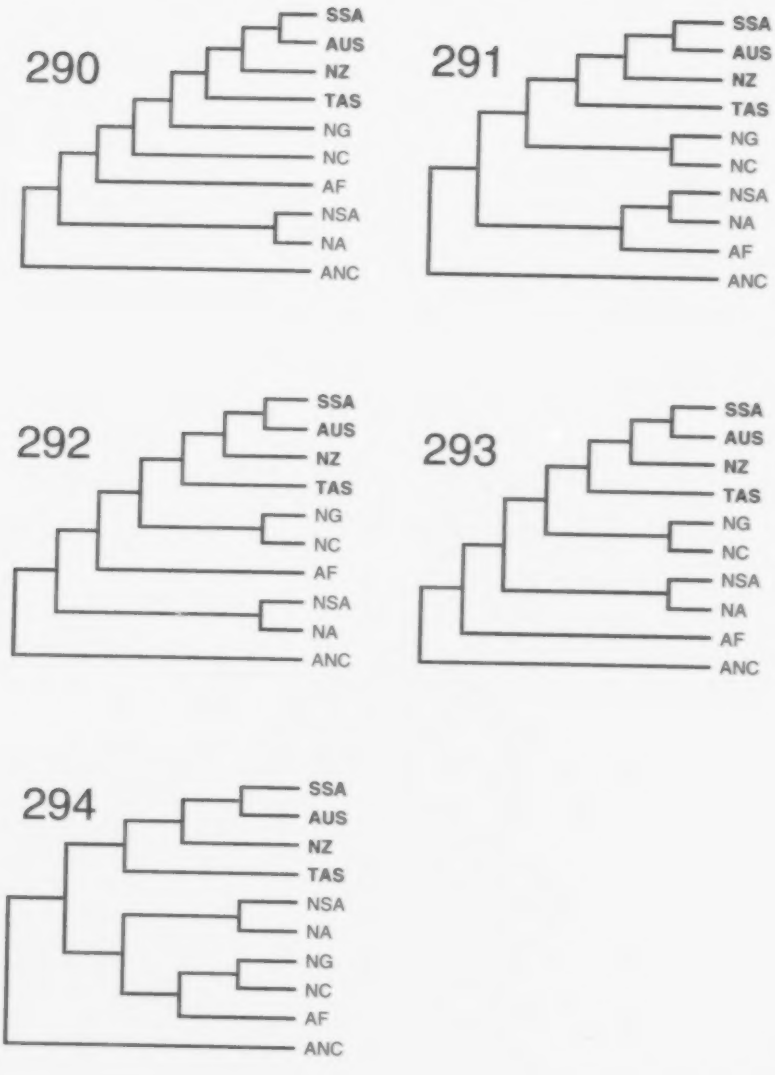
Figures 278-281. Area cladograms depicting the relationships among southern South America (SSA), northern South America (NSA), Australia (AUS), New Guinea (NG), New Caledonia (NC), Tasmania (TAS), New Zealand (NZ), South Africa (AF), and North America. Areas indicated in bold print are areas inhabited also by Pilipalpinae. **278**. Embothriinae (Proteaceae). **279**. Metallicina (Coleoptera: Carabidae). **280**. Siphlonuridae (Ephemeroptera). **281**. Nothofagus - Fagus (Fagaceae).



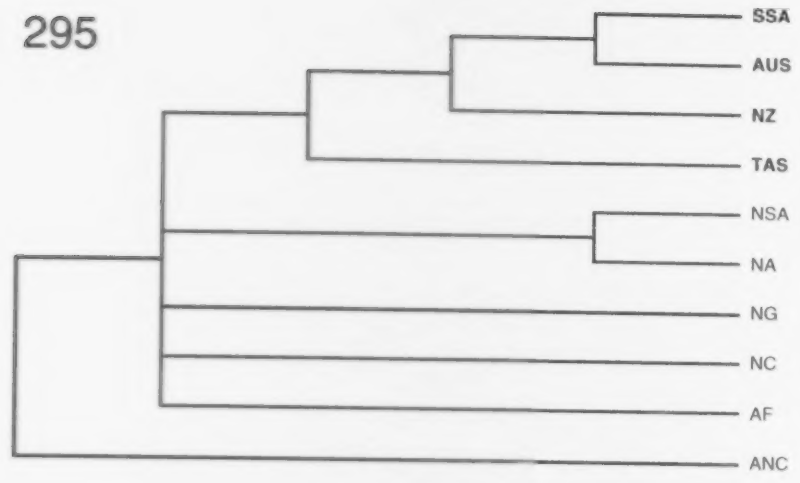
Figures 282-285. Area cladograms depicting the relationships among southern South America (SSA), northern South America (NSA), Australia (AUS), New Guinea (NG), New Caledonia (NC), Tasmania (TAS), New Zealand (NZ), South Africa (AF), and North America. Areas indicated in bold print are areas inhabited also by Pilipalpinae. **282**. Cyttaria (Cyttariaceae). **283**. Eriococcus - Madarococcus (Hemiptera: Eriococcidae). **284**. Negria - Drepanthus (Gesneriaceae). **285**. Oreomyrrhis (Apiaceae).

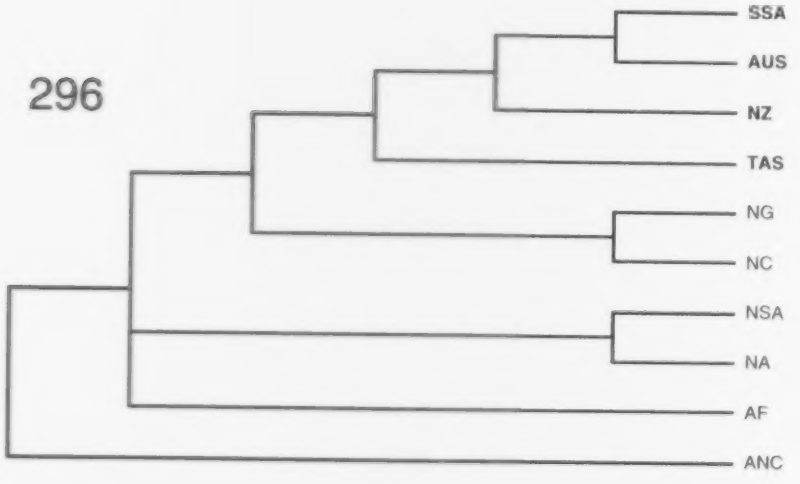


Figures 286-289. Area cladograms depicting the relationships among southern South America (SSA), northern South America (NSA), Australia (AUS), New Guinea (NG), New Caledonia (NC), Tasmania (TAS), New Zealand (NZ), South Africa (AF), and North America. Areas indicated in bold print are areas inhabited also by Pilipalpinae. **286**. Drapetes (Thymelaeaceae). **287**. Nannochoristinae (Mecoptera). **288**. Drimys (Winteraceae). **289**. Aristotelia (Elaeocarpaceae).



Figures 290-294. Five equally parsimonious trees computed from pooled Brooks Parsimony Analysis data (Table 6).





Figures 295-296. Strict (**295**) and majority rule (**296**) consensus trees computed from the five trees shown in Figs. 290-294.